**RESEARCH PAPER**

# 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.

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## INTRODUCTION

Unlike sessile species or those dwelling on islands, oceanic planktonic species have no apparent barriers to dispersal (Cermeño & Falkowski, 2009). It also appears that planktonic species are broadly distributed, both in space and in time.

Planktonic species also exhibit some of the most striking examples of explosive population growth (blooms) and of fine niche specialization (d'Ovidio *et al.*, 2010). Ecologists have long debated whether the regional distribution of species arises from dispersal limitation (MacArthur & Wilson, 1967) or from niche differentiation (Hutchinson, 1957). The neutral theory

of biodiversity (Hubbell, 2001) has generated a great deal of attention because it provides an integrative framework in which to test these alternatives (Duivenvoorden *et al.*, 2002). Initially, tests and applications of the neutral theory of biodiversity and biogeography had been restricted to tropical forests (e.g. Condit *et al.*, 2002; Duivenvoorden *et al.*, 2002; Chave *et al.*, 2006; Chust *et al.*, 2006a), but since then they have also been applied in marine ecology (e.g. Dornelas *et al.*, 2006; Martiny *et al.*, 2011) and more specifically to planktonic species assemblages (Alonso *et al.*, 2006; Pueyo, 2006a,b; Dolan *et al.*, 2007; Vergnon *et al.*, 2009; Irigoien *et al.*, 2011). However, these latter works have only partially tested the neutral model because they did not take into account explicitly the migration rate of species.

The neutral model of biodiversity developed by Hubbell (1997, 2001) was inspired by MacArthur & Wilson's (1967) theory of island biogeography. In Hubbell's model, all individuals are assumed to have the same prospects for reproduction and death (neutrality). The variability in relative abundances across species is solely due to demographic stochasticity or 'ecological drift'. This model further assumes a separation of spatial scales: demographic processes occur at the local scale of an ecological community, where species may go locally extinct through demographic drift. The local diversity is replenished by immigration at rate *m* of propagules from a regional species pool. In this large regional pool, drift may also cause species to go extinct, and novel species arise through speciation, such that θ new species are produced every generation in this regional pool. If *m* = 1, the local community is a random (Poisson) sample of the regional pool. In contrast, if *m* is close to zero, the local community is virtually isolated from the regional pool. Hubbell's neutral model thus assumes that limited dispersal, rather than niche specialization, is the main explanation for spatial structure across ecological communities. Under this model, the local species abundance distribution is thus defined by only two model parameters, θ and *m*. A spatially explicit version of Hubbell's model has also been developed (Chave & Leigh, 2002), in which dispersal from one locale to another is limited by the geographical distance between these sites. In such a model, taxonomic cross-site similarity (i.e. the opposite of β-diversity) declines logarithmically with increasing geographical distance (Hubbell, 2001; Chave & Leigh, 2002; Condit *et al.*, 2002).

In contrast, niche theory assumes that differences in species composition among communities is caused by heterogeneity in the environment or limiting resources, and by environmental filtering of species according to their environmental requirements, such as oceanographic conditions, and competition for resources such as nutrient concentrations for marine phytoplankton. In niche-based models, species are able to coexist by avoiding competition through resource and environmental partitioning (Gause, 1934; Chesson, 2000). Testing neutral theory against niche theory has proven challenging, because both environmental variables and species distributions tend to be spatially autocorrelated (Legendre *et al.*, 2005). On the one hand, species distributions are most often aggregated spatially because

of biotic processes such as reproduction and death. On the other hand, the pelagic environment is primarily structured by ocean currents and oceanographic processes causing spatial gradients. Statistical techniques have been developed to partition variation of diversity due to environmental variability and due to dispersal limitation (Legendre, 1993; Legendre *et al.*, 2005; Chust *et al.*, 2006b).

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

Here we examine the structure of communities of three phytoplankton groups (diatoms, dinoflagellates and coccolithophores), along a transect across the Atlantic Ocean from nearly 50° N to 50° S, to ascertain the extent to which the structure is consistent with niche assembly or dispersal (neutral) assembly. This latitudinal transect allows for large biological diversity and strong environmental gradients to be covered. All three phytoplankton groups behave as passive organisms and occupy the same trophic level. We seek to understand whether marine phytoplankton comply with neutral theory predictions of the distribution of relative species abundance and of spatial turnover in diversity. The following null hypotheses were formulated to address our main question: (1) According to the neutral theory, and when species are dispersal limited, the similarity of phytoplankton species composition should decrease with geographic distance, and the distance decay in similarity is expected to be more important than oceanographic conditions and nutrient concentrations. Here, we assess the relative contribution of dispersal limitation and environmental factors to the explanation of the variance in phytoplankton assemblages. We note that niche assembly mechanisms and neutral processes of drift and dispersal can occur simultaneously, so that results indicating a contribution of dispersal limitation, while supporting the neutral model, do not preclude a role for niche differentiation in phytoplankton assemblages. However, not finding a role of

dispersal limitation does not provide any information on the validity, or lack thereof, of the neutral model. (2) Assuming neutrality, the phytoplankton species abundance distribution should fit the distribution expected from Hubbell's neutral model. As the neutral theory applies to metacommunities, where local communities interact with each other by an immigration rate, the test has been performed in three regions (see also Cermeño *et al.*, 2010). Thus, we test, for the first time, the predictions of neutral theory for the spatial turnover in species composition and for relative species abundance in three of the most important phytoplankton groups.

## MATERIALS AND METHODS

### The AMT surveys and datasets

The Atlantic Meridional Transect (AMT) is an ocean observation programme that undertakes biological, chemical and physical oceanographic research over a latitudinal transect of the Atlantic Ocean from nearly 50° N to 50° S (Fig. 1), a distance of over 13,500 km (Robinson *et al.*, 2006). This transect crosses a range of biome types from subpolar to tropical and from eutrophic shelf seas and upwelling systems to oligotrophic
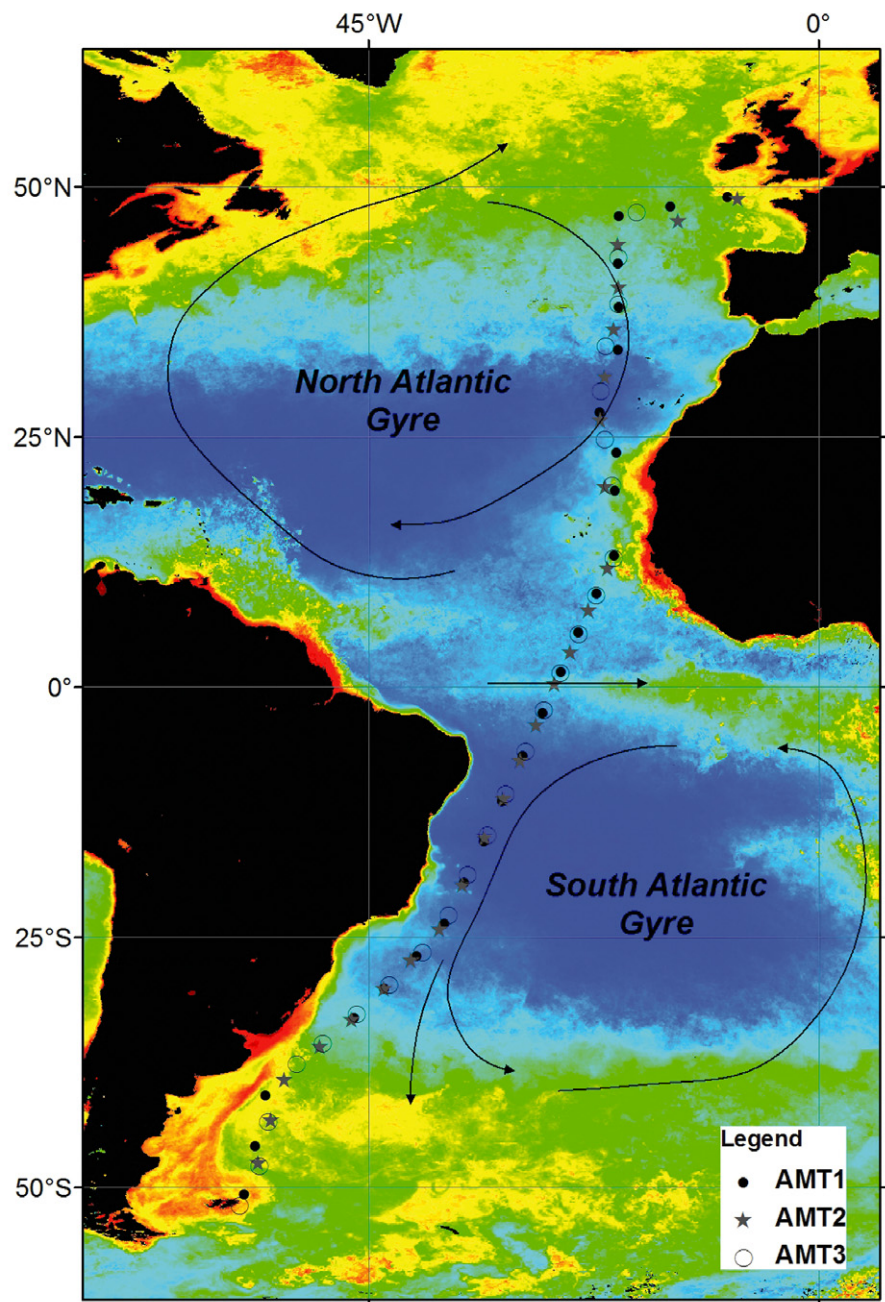


**Figure 1** Oceanographic sampling stations corresponding to AMT1, AMT2 and AMT3 (see Materials and Methods for details) overlain on a satellite image of ocean colour (blue, green, yellow and red represent increasing values of sea surface chlorophyll-*a* concentration; mean annual value for 2010, MODIS sensor). Arrows indicate the main Atlantic oceanographic gyres.

| | 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) | 683,648 | 23,282 | 94,110 |
| Abundance (AMT2) | 1,563,014 | 7120 | 109,535 |
| Abundance (AMT3) | 568,879 | 5674 | 104,262 |
| 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 |

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

mid-ocean gyres. We analysed phytoplankton data from the first three AMT surveys, on board the research ship *James Clark Ross*: AMT1 (which took place from 21 September to 24 October 1995), AMT2 (between 22 April and 28 May 1996) and AMT3 (between 20 September and 25 October 1996). The AMT1 and AMT3 surveys sailed from the UK to the Falkland Islands, whereas AMT2 sailed from the Falkland Islands to the UK. The AMT surveys included 25 sampling stations, each separated by 4° latitude from the next station.

Data from AMT surveys are available from the British Oceanographic Data Centre (BODC; http://www.amt-uk.org/data.aspx) and are described in Robins *et al.* (1996), Robins (1996) and Bale (1996). Specifically, chemical and phytoplankton data were sampled in waters at 7 m depth using a rosette (i.e. water sampling device) fitted with 12 10-l General Oceanics water bottles. Physical and optical data were obtained with a conductivity–temperature–depth probe (Neil Brown Mark IIIB, Neil Brown Instrument Systems, Inc., Cataumet, MA, US). Environmental data considered in our analysis encompass physical variables (sea surface temperature, salinity), optical variables [down-welling irradiance at photosynthetically active radiation (PAR) wavelengths, percentage of irradiance at sampling depth, surface solar radiation] and nutrients: nitrate + nitrite $(NO_3 + NO_2)$, nitrite $(NO_2)$, phosphate $(PO_4)$ and silicate $(SiO_4)$ concentrations. The percentage of surface irradiance at the sampling depth was inferred from the spectral diffuse attenuation coefficient of light ($K$) at PAR wavelengths. Geographic data were latitude and longitude.

For the collection and identification of phytoplankton, 100-ml samples were taken at each station and preserved in Lugol's iodine solution (Robins, 1996). Examination of the samples was conducted following Uthermol's sedimentation technique under an inverted microscope (Robins, 1996). The sampling procedure and volume used is the standard one for phytoplankton, considered adequate for repeatable characterizations of oceanic phytoplankton communities (Lund *et al.*, 1958). Previous studies using these three AMT datasets (and two others, AMT4 and AMT5) showed qualitatively similar productivity–diversity patterns, which indicates that 100-ml samples provide reasonable representation of the phytoplankton community diversity (e.g. Irigoien *et al.*, 2004). Phytoplankton (diatoms, dinoflagellates and coccolithophores) were taxonomically classified based on morphological characters at species level, and in some cases at genus level. For the present analysis, the species abundance per 100-ml sample volume was considered in order to work with count data (i.e. number of individuals). Overall, diatoms are the most diverse of the three phytoplankton groups (from 83 to 92 diatom species per survey, 35 to 42 dinoflagellate species, and 34–38 coccolithophore species; see Table 1). However, coccolithophores showed the highest average species richness per station (9.8), followed by diatoms (8.3) and dinoflagellates (6.5). Among coccolithophores, the most abundant species in all three surveys was the bloom forming *Emiliania huxleyi*. In contrast, the most abundant diatom and dinoflagellate species varied from one survey to the next. In particular, diatoms varied markedly in abundance and dominance; for instance the most abundant species on AMT1 was *Thalassiosira gracilis* with 6144.6 individuals ml$^{-1}$ but it was absent from both AMT2 and AMT3.

## Spatial species turnover

The relative contribution of environmental factors and geographic distance to phytoplankton composition was estimated using similarity matrices, Mantel tests and variation partitioning of the species composition across sites based upon canonical ordination methods (Legendre & Legendre, 1998). The Jaccard index was used to measure the compositional similarity between pairs of stations. The Jaccard index is the number of species shared between the two plots, divided by the total number of species observed. Distance matrices for environmental variables and geographic distance were measured by the Euclidean distance between values at two stations. We used Mantel tests (Legendre & Legendre, 1998) to determine the correlation between species similarity matrices and environmental and geographic distance. The Mantel test is a nonparametric test based on a boostrap randomization of the matrices, to determine how frequently the observed similarity would arise by chance. This test computes a statistic $r_M$ which measures the correlation between two matrices. The rate of change in species similarity with increasing geographic distance was calculated by fitting a linear model. Also, the latitudinal range of a species was defined as the distance between the observed latitudinal extremes of its occurrence. From the individual species ranges, average latitudinal ranges were then computed for each phytoplankton group. To test the correlation between species similarity and environmental distance, we first selected the best subset of environmental variables, such that the Euclidean distance of scaled environmental variables would have the maximum correlation with community dissimilarities, using the *vegan* package (Oksanen, 2011) implemented in the R 2.13.1 language (R Development Core Team, 2011). We then compared the $2^p - 1$ possible models, where $p$ is the number of environmental variables, for each AMT survey and phytoplankton group. Only environmental variables with values in all stations were considered in the initial model. Subsequently, a partial Mantel test was undertaken to determine the relative contribution of environmental distance (after model selection) and geographic distance in accounting for species variation.

We partitioned the variance of phytoplankton composition across stations to determine the relative contribution of environmental factors and spatial pattern. Species spatial patterns, as a result of aggregation because of biotic processes, were modelled with third-degree polynomial of geographic coordinates of latitude ($X$) and longitude ($Y$): $X$, $Y$, $XY$, $X^2$, $Y^2$, $X^2Y$, $Y^2X$, $X^3$ and $Y^3$ (cubic trend surface analysis, Legendre, 1993). The total inter-site variation in species abundance was decomposed into four components: pure effect of environment, pure effect of geographical distance, combined variation due to the joint effect of environment and geographical distance, and unexplained variation. Since partitioning on distance matrices (Mantel approach) underestimates the amount of variation in community composition (Legendre *et al.*, 2005), we used a canonical (i.e. constrained) ordination analysis (ter Braak & Šmilauer, 1998) to estimate a proportion of the variance of the original phytoplankton table of abundances (sites by species). Canonical ordination analysis is a method to reduce the variation in community composition in which the axes are constrained to be linear combinations of explanatory variables. More specifically, species are assumed to have unimodal response surfaces with respect to explanatory gradients. The variance partitioning analysis, detailed in Legendre *et al.* (2005), proceeds in two steps. First, we selected the best two canonical correspondence models (one for environmental variables, the other for spatial terms) using a stepwise procedure and based upon the Akaike information criterion (AIC), with the *vegan* package (Oksanen, 2011) implemented in the R 2.13.1 language (R Development Core Team, 2011). Subsequently, a partial canonical analysis (ter Braak & Šmilauer, 1998) was undertaken to determine the relative contribution of environmental factors and spatial terms in accounting for species variation. Specifically, the partial canonical analysis estimates the contribution of environmental factors in accounting for species variation by removing the effect of the spatial term covariable. Because of the presence of environmental missing values (at 29 sites) and low number of stations per AMT survey for this type of analysis, the variation partitioning was undertaken for the overall three AMT surveys (46 sites) restricting the analysis to six environmental variables whose values were available for all sites: sea surface temperature, salinity, percentage of irradiance, $NO_2$, $PO_4$ and $SiO_4$.

## Neutral theory

One radical step toward the construction of a mathematically tractable community model is Hubbell's theory of biodiversity (Hubbell, 2001). This theory is radical in its assumption that all individuals have the same prospects of reproduction and death irrespective of their age, size and of the species to which they belong. Hubbell (2001) modelled local communities in which each death is replaced with probability $1 - m$ by an offspring of a randomly chosen individual in the local community, regardless of species, and with probability $m$ by an immigrant from the regional species pool. The species of immigrant is determined by the relative abundance of species in the regional pool. In Hubbell's original model, community size remains constant, but in later versions the size of the local community can vary about a stochastic mean size (Volkov *et al.*, 2003). Hence, the species composition fluctuates due to stochastic drift only, but not because of habitat selection or interspecific competition. The local community is embedded in and connected via migration to the geographic area occupied by the regional species pool, the metacommunity, of size $J_M$ (the number of individuals in the regional pool), so that a fraction $m$ of recruits has immigrated from the regional pool rather than being the offspring of local parents. The local community reaches a dynamic equilibrium between stochastic local species extinction and species replenishment through immigration. At the scale of the regional pool, a similar dynamics occurs; diversity is maintained because extinction is balanced by speciation. Speciation in the regional species pool is modelled simply by assuming that each new recruit has a small probability $\nu$ of yielding an altogether new species, so that $\theta = \nu J_M$ new species appear in the system on average each generation. Hubbell's, (2001) neutral model, thus,

has two parameters: the regional diversity parameter θ and the immigration rate *m*. Etienne, (2005) has formally shown that θ can jointly be estimated with *m* from empirical species abundance data using a maximum likelihood framework.

Jabot & Chave (2011) have proposed a test of neutrality building upon Etienne's (2005) maximum-likelihood (ML) inference method. Briefly, for any species abundance distribution, a ML estimate of the neutral parameters θ and *m* may be obtained. Using Hubbell's model as a null model, neutral species abundance distributions are constructed, and only those with the same number of species as in the empirical dataset are retained, until one reaches 1000 simulated communities. These neutral species abundance distributions therefore have the same observed number of species and the same θ and *m* as do the empirical species abundance distribution. To build a test, Shannon's index is then calculated for both the neutral species abundance distributions and for the empirical one. The rationale for our choice of Shannon's index as a summary statistic is further explained in Jabot & Chave, (2011). If the empirical Shannon's index falls outside the distribution of neutral Shannon's indices, then neutrality is rejected. The empirical Shannon index was compared with this null distribution by a *t*-test. This test of neutrality is based on species abundance distributions only, but it is more robust than previous tests.

We explored the results of this neutrality test along the latitudinal axis by partitioning the global dataset into three regions: northern temperate zone (> 25°), tropical zone (between ≥ 25° and < 25°) and southern temperate zone (≤ 25°) (see Fig. 1). The boundary of the northern zone with the tropical coincides with the Westerlies biome and Trade Winds biome, respectively, defined by the Longhurst biogeographical provinces (VLIZ, 2009). The tropical zone so defined had a mean sea surface temperature above 24.5 °C (north of the equator) and above *c.* 22 °C (south of the equator).

We estimated the neutral model parameters θ and *m* together with confidence intervals and also performed the above test for the total dataset (including diatoms, coccolithophores and dinoflagellates). This inference was implemented in the TETAME software (Jabot *et al.*, 2008). Of the 75 samples, eight had more than 50,000 individuals, and this resulted in prohibitively long calculations (akin to finding the zeros of a polynomial of degree equal to the number of individuals; see Etienne, 2005). For these eight samples, we picked a random sample of 50,000 individuals and replicated this sampling procedure 10 times to ensure its stability. In two cases, the neutral parameters could not be computed due to sample sizes that were too small. In a majority of tests, neutrality was not rejected; in such cases, assuming neutrality, we explored how the estimated immigration probability (*m*) varied with latitude throughout the main Atlantic zones.

## RESULTS

### Spatial species turnover

Mean similarity among stations was highest for coccolithophores (0.29), followed by dinoflagellates (0.23) and diatoms
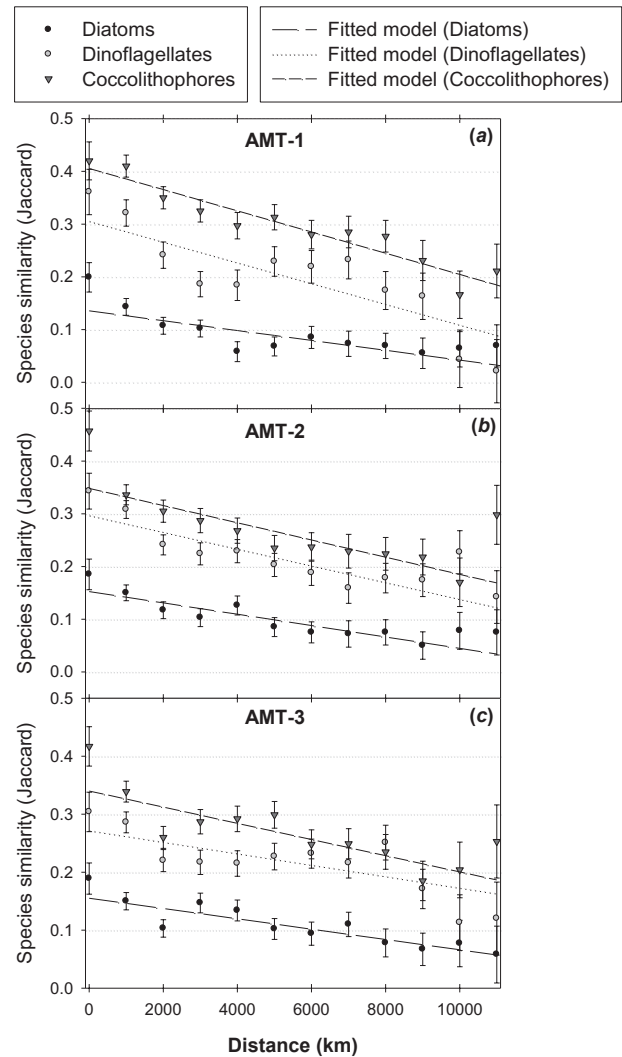


**Figure 2** Species similarity against the distance between stations for each AMT (AMT-1 in (a), AMT-2 in (b), and AMT-3 in (c)), and for the three phytoplankton groups (diatoms, dinoflagellates and coccolithophores). Species similarity was averaged at 1000-km intervals. Error values are the standard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

(0.11) (see Table 1). The geographic distance range occupied by a species (on average) is less in diatoms (3352.8 km) than in dinoflagellates (4784.1 km) and coccolithophores (6093.8 km) (Table 1). Similarity of the three phytoplankton groups decreases significantly ($P < 0.001$) in all three groups with geographic distance [Fig. 2; $r_M$ (diatoms) = 0.24–0.28; $r_M$ (dinoflagellates) = 0.20–0.34; $r_M$ (coccolithophores) = 0.29–0.39] and in all three AMT surveys. The Mantel correlation between species similarity and environmental factors (0.37–0.74) was higher than with geographic distance (0.21–0.39), for the three phytoplankton groups and the three surveys (Table 2). The Mantel correlation between species similarity and geographic distance, partialling out environmental factors, was significant ($P < 0.05$) for a majority of cases (in all three groups for AMT1 and AMT2).

Table 2 Mantel and partial Mantel tests between species similarity and environmental determinants and geographical distance, for each AMT (Atlantic Meridional Transect) survey and phytoplankton group.

| | | | Mantel $r$ | $P$-value | Terms selected | Terms entered |
|---|---|---|---|---|---|---|
| AMT1 | Diatoms | Jacc × Environ. | 0.42 | 0.001 | Temperature, irrad | $NO_3 + NO_2$, $NO_2$, $PO_4$, salinity, $SiO_4$, temperature, irrad |
| | | Jacc × Distance | 0.25 | 0.001 | | |
| | | Jacc × Environ. (Distance partially out) | 0.38 | 0.001 | | |
| | | Jacc × Distance (Environ. partially out) | 0.15 | 0.009 | | |
| | Dinoflag. | Jacc × Environ. | 0.58 | 0.001 | $NO_2$ | $NO_3 + NO_2$, $NO_2$, $PO_4$, salinity, $SiO_4$, temperature, irrad |
| | | Jacc × Distance | 0.33 | 0.001 | | |
| | | Jacc × Environ. (Distance partially out) | 0.53 | 0.001 | | |
| | | Jacc × Distance (Environ. partially out) | 0.14 | 0.047 | | |
| | Coccolith. | Jacc × Environ. | 0.74 | 0.001 | $NO_2$, temperature | $NO_3 + NO_2$, $NO_2$, $PO_4$, salinity, $SiO_4$, temperature, irrad |
| | | Jacc × Distance | 0.39 | 0.001 | | |
| | | Jacc × Environ. (Distance partially out) | 0.68 | 0.001 | | |
| | | Jacc × Distance (Environ. partially out) | 0.15 | 0.030 | | |
| AMT2 | Diatoms | Jacc × Environ. | 0.38 | 0.001 | Temperature | $NO_3 + NO_2$, $NO_2$, $PO_4$, salinity, $SiO_4$, temperature, irrad, sol |
| | | Jacc × Distance | 0.29 | 0.001 | | |
| | | Jacc × Environ. (Distance partially out) | 0.32 | 0.001 | | |
| | | Jacc × Distance (Environ. partially out) | 0.19 | 0.005 | | |
| | Dinoflag. | Jacc × Environ. | 0.37 | 0.001 | $NO_2$, temperature | $NO_3 + NO_2$, $NO_2$, $PO_4$, salinity, $SiO_4$, temperature, irrad, sol |
| | | Jacc × Distance | 0.34 | 0.001 | | |
| | | Jacc × Environ. (Distance partially out) | 0.23 | 0.005 | | |
| | | Jacc × Distance (Environ. partially out) | 0.18 | 0.004 | | |
| | Coccolith. | Jacc × Environ. | 0.60 | 0.001 | Temperature | $NO_3 + NO_2$, $NO_2$, $PO_4$, salinity, $SiO_4$, temperature, irrad, sol |
| | | Jacc × Distance | 0.32 | 0.001 | | |
| | | Jacc × Environ. (Distance partially out) | 0.55 | 0.001 | | |
| | | Jacc × Distance (Environ. partially out) | 0.16 | 0.014 | | |
| AMT3 | Diatoms | Jacc × Environ. | 0.46 | 0.001 | Temperature | Salinity, temperature |
| | | Jacc × Distance | 0.24 | 0.004 | | |
| | | Jacc × Environ. (Distance partially out) | 0.41 | 0.001 | | |
| | | Jacc × Distance (Environ. partially out) | 0.07 | 0.199 | | |
| | Dinoflag. | Jacc × Environ. | 0.47 | 0.001 | Temperature | Salinity, temperature |
| | | Jacc × Distance | 0.21 | 0.011 | | |
| | | Jacc × Environ. (Distance partially out) | 0.43 | 0.001 | | |
| | | Jacc × Distance (Environ. partially out) | 0.04 | 0.323 | | |
| | Coccolith. | Jacc × Environ. | 0.56 | 0.001 | Temperature | Salinity, temperature |
| | | Jacc × Distance | 0.29 | 0.001 | | |
| | | Jacc × Environ. (Distance partially out) | 0.51 | 0.001 | | |
| | | Jacc × Distance (Environ. partially out) | 0.10 | 0.091 | | |

irrad, irradiance; sol, solar radiance; Jacc, Jaccard index.

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

## Neutral theory parameters and test

The estimates of neutral parameters ($\theta$ and $m$) for each station are shown in Table 3 for the three defined latitudinal regions (see also Appendix S1 in Supporting Information for parameters
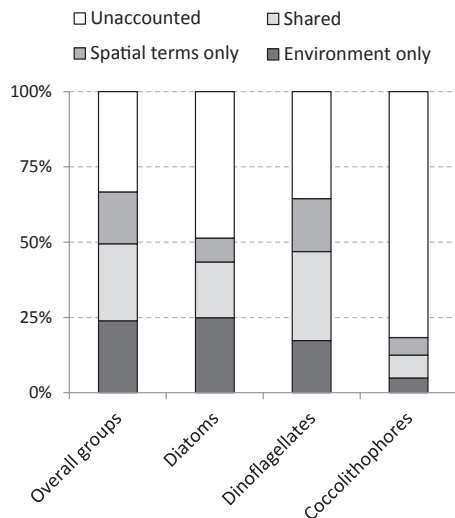
**Figure 3** Variation partitioning (%) of species composition, based on constrained correspondence analysis, according to spatial terms and environmental determinants, for each phytoplankton group.

for each station). The test of fit of the phytoplankton species abundance distribution to the neutral communities indicates that the number of communities in which neutrality cannot be rejected is higher (45) than the number in which neutrality can be rejected (28) (Table 3). Communities for which neutrality could not be rejected made up a larger percentage of tropical communities (50 to 100%), than of communities in the northern (40 to 57%) or southern (17 to 71%) zones. Figure 4 shows six examples of the empirical species abundance distribution compared with that expected by a neutral model given the local community parameters θ and *m*. These examples are representative of communities in all three latitudinal zones and illustrate variation in the goodness of fit of the neutral expectation. Those communities whose abundance distributions were not fit by the neutral model (e.g. Fig 4b,d,f), generally exhibit too many species in the abundance classes of 3 to 16 individuals per species.

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

## DISCUSSION

We tested two predictions of neutral theory against data on the community structure of three marine phytoplankton groups in a latitudinal transect of the Atlantic Ocean. First, the canonical ordination analysis and Mantel tests showed that environment and geographic distance explained variation in diversity for the three phytoplankton taxa (diatoms, dinoflagellates and coccolithophores). These analyses also indicated that environment is slightly more important than geographic distance. Second, the Shannon information test of the fit of neutral theory to observed relative species abundance distributions showed that neutral expectations cannot be rejected for 60% of communities. These two findings suggest that phytoplankton communities result from a combination of niche and neutral processes, which is in accordance with the patterns found in an exhaustive phytoplankton time-series dataset (Vergnon *et al.*, 2009). Similar conclusions were reached in a study of phytoplankton communities in the Caribbean and Mediterranean seas; Pueyo (2006a) states that both neutral and non-neutral mechanisms co-occur. These recent findings and the results of this paper lead to a new perspective, that niche assembly is not the only, or even always the prevailing, assembly mechanism of plankton communities, in contrast to the views that emerge from previous, global-scale studies of fossil diatom assemblages (Cermeño & Falkowski, 2009). To the best of our knowledge, ours is the only approach to combine three important analyses of the same dataset: (1) empirical estimation of dispersal limitation, (2) assessment of the relative contribution of environmental factors and dispersal limitation to community assembly; and (3) estimation of migration rate in the neutral model.

The estimation of dispersal limitation revealed slight differences between phytoplankton groups. On the one hand, the geographic distance range occupied by one species (on average) is less in diatoms than in dinoflagellates and coccolithophores (Table 1). This suggests that connectivity among population sites is low in diatoms. On the other hand, coccolithophore similarity has a correlation with geographic distance (i.e. distance decay) slightly higher (0.29–0.39) than in diatoms (0.24–0.28), which can be interpreted as high spatial structuring (i.e. patchiness). In a pure neutral metacommunity, high slopes in the distance decay and small ranges of geographic distance occupied by the species are related and provide a measure of dispersal limitation. In our case, however, diatoms have the lowest latitudinal range and the lowest distance decay slope. This apparent paradox should be due to the fact that diatom occurrences are very low (two to three stations on average per AMT survey), with respect to coccolithophores (more than seven). The differential abundance of species, and differing species richness, make it difficult to evaluate the significance of small differences in dispersal in the different groups. Although mobility, sedimentation and growth rates are known to differ among these phytoplankton groups (Broekhuizen, 1999), their functional similarity and co-occurrence in similar environments might result in similar dispersal rates at the community level. This is an aspect that requires further research. A limitation of our dataset is that samples were not repeatedly subsampled, to test for repeatability and the degree to which the species diversity present was accurately represented (Gotelli & Colwell, 2001). The difficulties of detecting the smallest organisms and

**Table 3** Test of fitting phytoplankton species abundance distribution (SAD) to the neutral model for the three AMT surveys and zones.

| | Zone | Number of stations | S | n | H | θ | 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 |
| Overall | | 73 | | | | | | 45 |

$S$, species richness; $n$, total number of individuals; $H$, Shannon's index of diversity; $θ$, the fundamental biodiversity parameter; $m$, species immigration probability of a local community from the metacommunity. $S$, $H$, $θ$ and $m$ are the mean values for the corresponding zone. See Appendix S1 for values for each station.

**Figure 4** Empirical species abundance distributions and that expected under neutral model of six communities using Preston plots. Grey bars show the binned abundance classes (i.e. 1, 2, 3–4, 5–8, 9–16, . . . ), and black circles represent the expected number of species for each abundance class under a neutral model with maximum likelihood estimation of parameters $θ$ and $m$, and $J$ individuals. (a) Northern station AMT3.4 ($J = 2294$, $θ = 3.75$, $m = 0.45$, $P = 0.114$). (b) Northern station AMT1.4 ($J = 3224$, $θ = 3.46$, $m = 0.52$, $P = 0.003$). (c) Tropical station AMT3.9 ($J = 1548$, $θ = 3.91$, $m = 0.26$, $P = 0.344$). (d) Tropical station AMT3.12 ($J = 7052$, $θ = 3.82$, $m = 0.54$, $P = 0.009$). (e) Southern station AMT2.5 ($J = 3436$, $θ = 7.69$, $m = 0.099$, $P = 0.167$). (f) Southern station AMT1.20 ($J = 2692$, $θ = 4.63$, $m = 0.44$, $P < 0.001$). Communities on the left side (a, c and d) were fitted to neutral model according to the test ($P > 0.05$), and communities on the right (b, d and f) did not fit to the neutral model ($P < 0.05$).
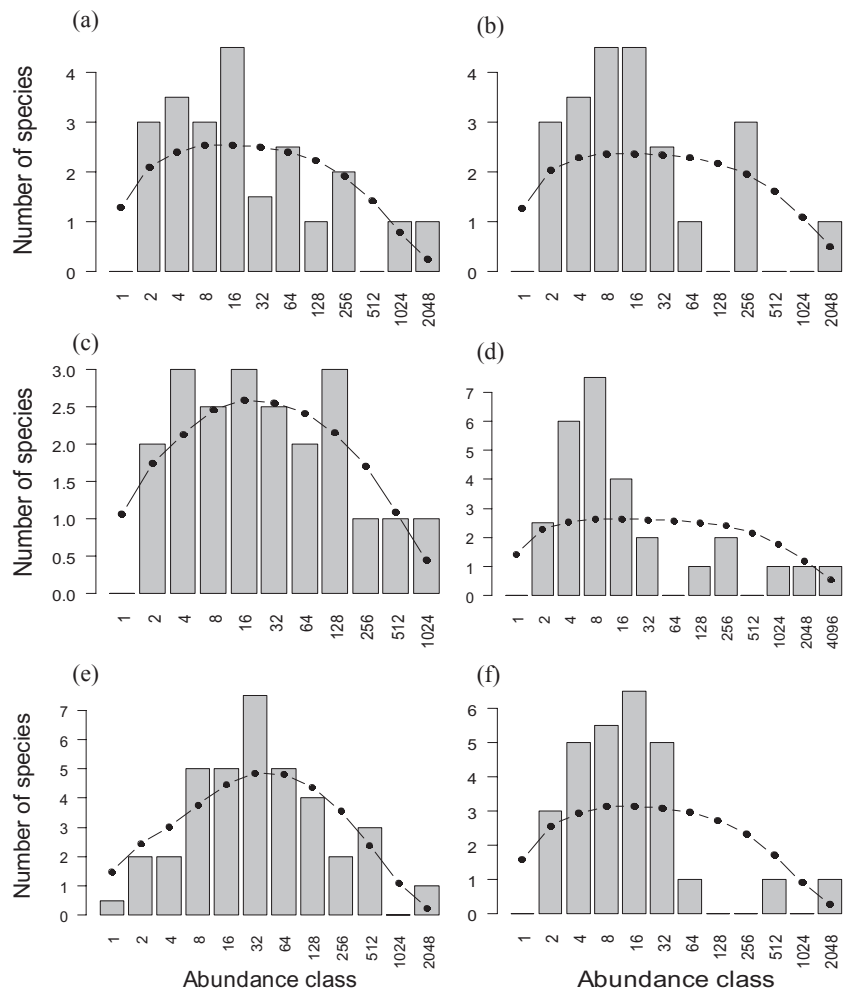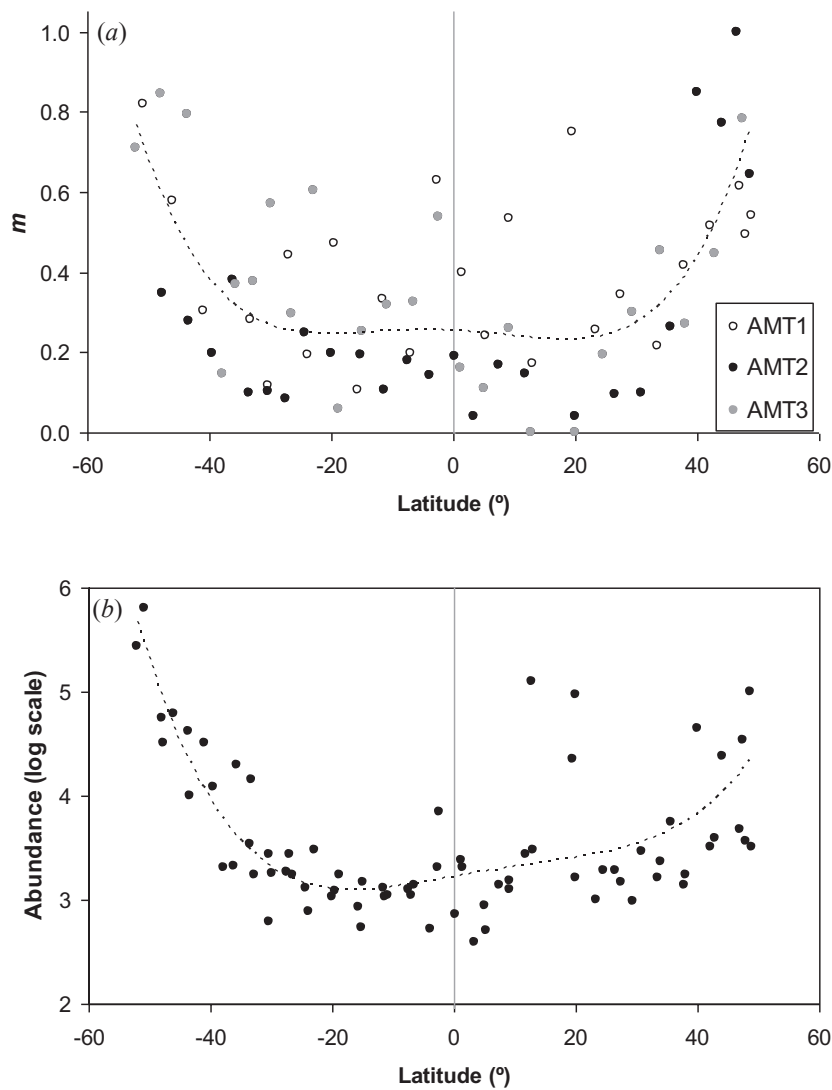
Figure 5 (a) Immigration rate (*m*) and (b) overall abundance across latitude for each AMT survey. The fitted curve is a fourth-order polynomial model (for *m*, $r^2 = 0.44$, $P < 0.0001$; for abundance, $r^2 = 0.54$, $P < 0.0001$), selected with the Akaike information criterion comparing four polynomial models from first to fourth order.

capturing the largest organisms, which are rare in finite volumes, are always problematic (e.g. Vergnon *et al.*, 2009). However, the consistent patterns between AMT surveys in our analysis and previous studies (Irigoien *et al.*, 2004) allow us to conclude that community diversity is well captured and sampling biases are not important.

The three phytoplankton groups exhibited differences in community metrics, but similar patterns between AMT surveys. Coccolithophores are more diverse in the tropical zone, decreasing slightly with latitude (see Appendix S2). Over the entire geographic dataset, they are less diverse than diatoms, although local (per sample) diversity is higher than that of diatoms. Both abundance and the number of species of coccolithophores are very constant across latitudes, compared with diatoms and dinoflagellates. Concerning the strength of the species response to the environment, canonical ordination analysis and Mantel tests were consistent in that the environment is slightly more important than geographic distance, although the results of the two statistical analyses differ slightly at the group level. At the current relatively coarse level of analysis it is not possible to

determine which phytoplankton group responds most strongly to environment. The current wisdom is that diatoms are *r*-strategists associated with mixed waters and unpredictable conditions (e.g. Margalef, 1978). However, all three taxa exhibit massive blooms, generally taking place in temperate, mixed water zones (Fig. 5b). In each of the three taxa, there is a single species responsible for blooms: among diatoms it is *Thalassiosira gracilis*, among dinoflagellates it is *Gymnodinium galeaeformae* and among coccolithophores it is *Emiliania huxleyii*, similar to the findings of Irigoien *et al.* (2004). During these massive bloom situations, species richness decreases (Appendix S3), in agreement with previous studies (e.g. Irigoien *et al.*, 2004), which is here interpreted as competitive exclusion (Huisman *et al.*, 1999) because of limiting resources. If this is the case, these exceptional situations escape from the assumptions of neutral theory.

In comparison with other ecosystems, the pelagic environment and remote islands (e.g. islands *sensu stricto*, caves, basins, lakes, estuaries, forest remnants) are the two opposite extremes in terms of population connectivity. Whereas islands

could be considered as adimensional points where connectivity is very limited, the pelagic zone could be seen as a three-dimensional space with no barriers for marine plankton (Cermeño & Falkowski, 2009) except those imposed by physical heterogeneity (e.g. stratification) and continents. From this point of view, i.e. increasing space dimensions increases potential connectivity, land could act as a two-dimensional space for sessile species (e.g. plants), whereas coastlines can limit the dispersal of their inhabitants (e.g. restricted intertidal organisms) in one dimension. For instance, whereas coastal fish species are more likely to remain close to their place of origin, oceanic animal species are highly mobile and live in a continuous habitat with high connectivity (Tittensor *et al.*, 2010). Within this general framework, our findings reveal, nevertheless, that overall phytoplankton assemblages are poorly but consistently spatially structured across the Atlantic, indicating that dispersal limitation is playing a non-negligible role in global distribution of oceanic primary producers. Our results on dispersal limitation and spatial community structure are intermediate between the strong barriers to dispersal evident in thermophilic Archaea (Whitaker *et al.*, 2003), and the other extreme of no limits to dispersal, expressed in the view that below 1 mm body size 'everything is everywhere, but the environment selects' (Finlay, 2002). Unlike terrestrial plants, for which ecological drift is potentially a key factor on regional scales, marine phytoplankton species are nearly pan-distributed over all latitudes (at least for species described at the morphological level). Whether the morphologically described species include cryptic species (e.g. Kooistra *et al.*, 2008) or ecotypes with adaptations at the molecular level (e.g. Johnson *et al.*, 2006), and to what extent the consideration of those would improve the percentage of the variance explained by the environment, is an aspect that requires further research.

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

## CONCLUSION

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

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

**Appendix S1** Test of fitting phytoplankton species abundance distributions to the neutral model for the each sampling station.
**Appendix S2** Latitudinal patterns of sea surface temperature, salinity and species richness of diatoms, dinoflagellates and coccolithophores.
**Appendix S3** Unimodal relation of phytoplankton species richness across biomass and abundance.

### BIOSKETCH

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Editor: Carlos M. Duarte