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Nestedness pattern in stream diatom assemblages of central Western Ghats

B. Karthick[1], M. K. Mahesh[2] and T. V. Ramachandra[1,*]

[1]Energy and Wetlands Research Group, Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560 012, India
[2]Department of Botany, Yuvaraja's College, Mysore 570 005, India

Community diversity and the population abundance of a particular group of species are controlled by immediate environment, inter- and intra-species interactions, landscape conditions, historical events and evolutionary processes. Nestedness is a measure of order in an ecological system, referring to the order in which the number of species is related to area or other factors. In this study we have studied the nestedness pattern in stream diatom assemblages in 24 stream sites of central Western Ghats, and report 98 taxa from the streams of central Western Ghats region. The communities show highly significant nested pattern. The Mantel test of matrix revealed a strong relationship between species assemblages and environmental conditions at the sites. A significant relationship between species assemblage and environmental condition was observed. Principal component analysis (PCA) indicated that environmental conditions differed markedly across the sampling sites, with the first three components explaining 78% of variance. Species composition of diatoms is significantly correlated with environmental distance across geographical extent. The current pattern suggests that micro-environment at regional levels influences the species composition of epilithic diatoms in streams. The nestedness shown by the diatom community was highly significant, even though it had a high proportion of idiosyncratic species, characterized with high numbers of cosmopolitan species, whereas the nested species were dominated by endemic species. PCA identifies ionic parameters and nutrients as the major features which determine the characteristics of the sampling sites. Hence the local water quality parameters are the major factors in deciding the diatom species assemblages.

*For correspondence. (e-mail: cestvr@ces.iisc.ernet.in)

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IN an era of human impact on natural ecosystems, a major challenge for ecologists is to understand the structure and dynamics of biological communities in relation to environmental variability[1]. Community diversity and the population abundance of a particular group of species are controlled by immediate environment, landscape conditions, inter- and intra-species interactions, historical events and evolutionary processes[2–5]. The diversity of community is not only important from basic science of ecology, but is also fundamental to conservation biology[6]. Although attempts to understand the spatial patterns have been documented in many studies of plant and animal diversity, it has not been done for microbial species. This is a serious omission given that microorganisms constitute much of the biodiversity on earth[7] and have vital functional roles in biogeochemical cycles as well as ecosystem functioning[8,9]. With limited information on macro-ecological patterns of micro-organisms, theories were built and tested, but lack facts[10]. However, Martiny *et al.*[11] concluded that microbial diversity is partly decided by the environment and the processes that generate and maintain biogeographic patterns in macroorganisms could operate in the microbial world.

Diatoms (division Bacillariophyta), one of the largest groups of microorganisms, are among the most successful groups of photosynthetic eukaryotic microorganisms. They occur in almost all wet/damp places with a diverse range of habitats across the continents. Diatoms grow as single cells, or form simple filaments/colonies. They form the base of aquatic food webs in marine and freshwater habitats. Diatom species are sensitive to the physical and chemical parameters of water such as pH, nutrients, salinity, temperature and water current in which they live. As a result, they are used extensively in environmental assessment and monitoring across the globe. Like many other microorganisms diatoms are least studied, particularly from the tropical regions. Recently, there have been a few studies from the temperate region analysing the spatial patterns[12,13] and assemblage patterns[14] of diatoms. These studies emphasize the importance of dispersal and migration in structuring diatom communities at regional to global scales, giving consideration to the regional diatom pool and habitat availability.

Considering the meagre understanding of species assemblage patterns of tropical streams, we attempted to study the nestedness pattern in stream diatom assemblages of central Western Ghats. There are several methods available to measure patterns in the species assemblages; with nestedness being a popular method for a wide range of taxa. Nestedness is a measure of order in an ecological system, referring to the order in which the number of species is related to area or other factors. The more a system is 'nested', the more it is organized. In general, the species assemblages are associated with species–area relationship, known as the 'nested subsets' pattern[15]. The nested subset pattern arises because species differ in their distribution across space. Some species use a wider range of resources or persist across a wider range of habitats than others[16–18]. Generally, species that use a wide range of resources or tolerate a variety of abiotic conditions can establish more populations in more places than comparable species with relatively narrow niches[19,20]. However, factors affecting the degree to which species are nested or idiosyncratic are poorly understood.

Analysing the nestedness pattern using the nestedness calculator was proposed by Patterson and Atmar[21], which further led to an increase in interest in this analysis (referred in 339 research papers as on 31 October 2009; ISI database search). It works with a combination of a thermodynamic measure of order and a Monte Carlo simulation[22]. A detailed account of the nestedness calculator and its application is available in Puyravaud *et al.*[23]. Many studies have revealed that variations in species assemblages can reflect nested distribution patterns[14,15,24–32]. A majority of these studies conclude that nestedness pattern exists due to selective extinction by which species disappear from different habitats in roughly the same order[33]. However, Cook and Quin[20] proposed that nested pattern develops in an ecosystem due to differential colonization abilities of species.

Identifying the nested assemblage patterns of freshwater diatoms in the streams of central Western Ghats and understanding the possible drivers for such patterns are the primary objectives of this communication.

Twenty-four stream sites comprising only first and second streams from central Western Ghats (Figure 1) were sampled during October 2007–February 2008 (post-monsoon season) using a strictly standardized field protocol[34]. The stream sites belong to three ecoregions of the Western Ghats, viz. Sawanthwadi–Kayna valley, Aghanashini–Terikhol valley and Pushpagiri–Sharavathi valley, from the river basins of Netravathi, Seethanadi, Swarna, Gurupur, Sharavathi, Aghanashini, Bedthi, Kali, Mandavi, Terekhol and Krishna. At each site three–five stones were selected randomly across the stream. Diatoms were scraped-off these stones as subsamples using a tooth brush. Subsequently, the subsamples were pooled into a composite sample for each site. Fresh samples were carefully checked to guarantee that most diatom frustules were alive before acid combustion. Almost all diatom cells had cytoplasmic content, and thus hot HCl and $KMnO_4$ method[34] was used to obtain clean frustules devoid of organic material. The cleaned diatoms were mounted in Pleurax for further microscopic analysis. A total of 400 frustules per sample were identified and counted using compound light microscopy (magnification 1000×). Diatoms were identified primarily to the species level, according to methods described earlier[35–37].

Water quality variables such as pH, water temperature (°C), total dissolved solids (mg l^{-1}), salinity (mg l^{-1}) and nitrates (mg l^{-1}) were recorded at the sampling sites using EXTECH COMBO electrode and Orion ion selective electrode. Other parameters like chloride, hardness, magnesium, calcium, sodium, potassium, sulphates and phosphates were analysed in the laboratory. All analyses were carried out according to standard methods for the examination of water[38].

A presence–absence matrix (matrix having sites in rows and species in columns, with 1 for presence and 0 for absence) was constructed for nestedness calculation. The degree of nestedness was calculated using the nestedness calculator[39,40]. The metric T of the 'nestedness

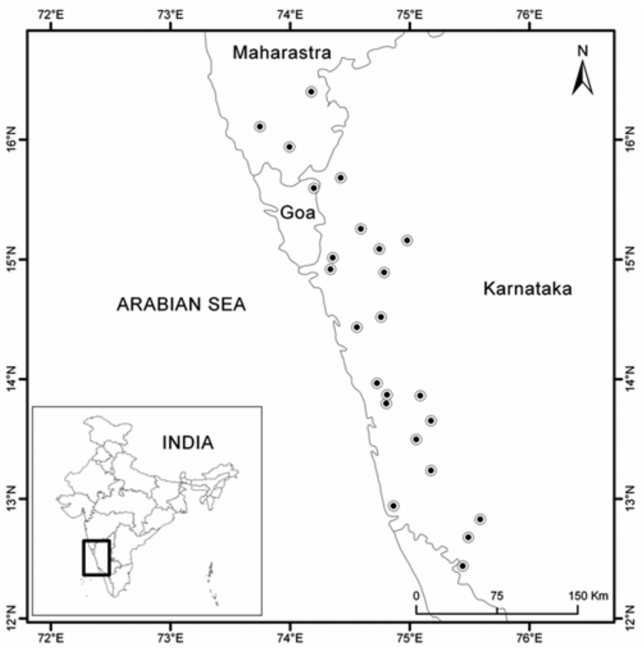

Figure 1. Map of central Western Ghats showing the sampling sites.

calculator' measures the extent of unexpected presence and absence in a maximally packed matrix, where sites are arranged in rows in descending order according to their species richness, and species are arranged in columns according to the number of sites on which they occur. The metric $T = 0°$ for a set of perfectly nested assemblages, and $T = 100°$ for completely disordered ones. The null hypothesis that T is not lower (i.e. more nested) than expected by chance, was tested using Monte Carlo permutations[41].

Mantel test correlations were used to elucidate the role of environmental and spatial factors in determining the species assemblages. The Mantel test estimates the intensity of the relationship between two variables and calculates a statistic that is similar to Pearson's correlation coefficient (r). The value of the Mantel statistic can vary from −1 to +1, and is typically calculated between two matrices, each containing the distance (or similarity) elements calculated for each pair of values of a variable. Partial Mantel test is used to examine the influence of environmental factors on diatom assemblages while holding geographical distance constant[42] and vice versa with 1000 permutations using the statistical package R[43]. Principal component analysis (PCA) was performed using R to elucidate the important physical and chemical water quality variables. The relationships between matrices of distance in species assemblages (using Bray–Curtis quantitative distance measure), environmental distance (matrix of Euclidean distances of ranked values of individual parameters) and geographic distance of the localities (aerial distances in kilometres calculated using Mapinfo 7.5 between sampling localities) were used in Mantel and partial Mantel test[44].

The present study reports 98 taxa from the streams of central Western Ghats region. The communities show highly significant nested pattern ($T = 16.41°C$ $P = 4.43e\text{-}31$, matrix fill = 14%) and mean $T = 50.61$ (± 2.88)°C derived from 1000 randomized matrices (Figure 2). The matrix consists of more nested species (66%). Highly nested species in this dataset include *Gomphonema gandhii* Karthick and Kociolek, *Navicula rostellata* Kützing, *Surirella* sp., *Nitzschia reversa* W. Smith, *Nitzschia sigma* (Kützing) W. Smith, *Navicula viridula* (Kützing) Kützing, *Eunotia bilunaris* (Ehrenberg) Souza in Souza and Moreira-Filho, *Caloneis silicula* (Ehrenberg) Cleve and *Pinnularia acrosphaeria* (Brébisson) W. Smith.

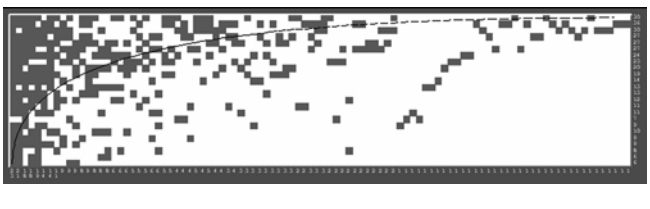

Figure 2. Species distribution matrix in 24 streams in central Western Ghats. The line indicates the maximally cold matrix.

Highly idiosyncratic species in this dataset are *Gomphonema* sp., *Achnanthidium minutissimum* (Kützing) Czarnecki, *Nitzschia palea* (Kützing) W. Smith, *Brachysira neoexilis* Lange-Bertalot, *Planothidium frequentissimum* Lange-Bertalot and *Planothidium* sp. Compared to the nested species, idiosyncratic species have wide ecological tolerance and are cosmopolitan in distribution; in particular species like *N. palea* are known to be present even in highly eutrophic water. Species such as *A. minutissimum* are known to occur only in oligotrophic water. Highly nested species in this dataset are probably endemic taxa (*G. gandhii* and *Surirella* sp.), apart from some cosmopolitan species.

The Mantel test of matrix revealed a strong relationship ($P = 0.001$) between species assemblages and environmental conditions at sites, which are physical and chemical properties of the water. There was no significant relationship between the species assemblage or the environmental condition and geographical distance. Moreover, the relationship between species assemblage and environmental condition was highly significant ($P = 0.002$) keeping geographical distance as constant in partial Mantel test. However, the species assemblage was not significantly correlated with geographical distance, keeping environmental condition as constant (Figure 3). In other words, closer localities did not have similar diatom species assemblages compared to the more distant ones (Table 1).

According to PCA analysis, the first, second and third principal axis captured 57.8%, 11.2% and 9.05% variance respectively (Table 2). PCA indicated that environmental conditions differed markedly across the sampling sites, with the first three components explaining 78% of variance. PC1 represents the increase in ionic characters like electrical conductivity, alkalinity, chlorides, calcium, sodium and potassium, whereas PC2 reflected an increase in magnesium, phosphates and nitrates and a decrease in dissolved oxygen.

The degree of nestedness was significant in these datasets ($T = 16.41°C$, $P = 4.43e\text{–}31$, matrix fill = 14%), with nearly 40% of species being idiosyncratic. Compared to temperate diatoms showing much higher nestedness[14] ($T = 28.4°C$), the tropical diatom assemblages in the present study were colder, which is attributed to the similar environmental condition of the sampled sites that determines the species assemblages.

The idiosyncrasy is greater in aquatic organisms compared to terrestrial organisms, which may be due to high dispersal ability of aquatic organisms[25]. This would probably increase matrix temperature as indicated in stream fish community[32] and lake molluscs[41]. Hence, the relatively high degree of idiosyncrasy observed in the present study, is not an exception in the aquatic ecosystem, particularly in eukaryotic assemblages. It is also possible that smaller the organism, higher is the temperature, which is due to greater dispersal ability and adaptive

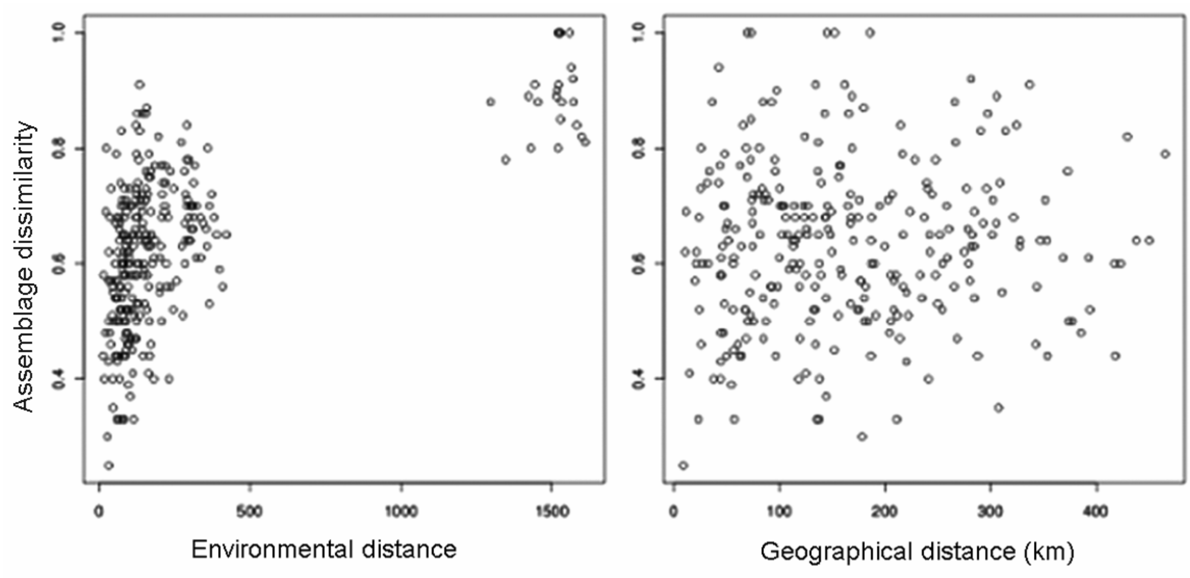

Figure 3. Relation of species assemblage dissimilarity with the environmental and geographical distances.

Table 1. Results of Mantel and partial Mantel tests for relationship between species assemblage dissimilarity, and environmental and geographical distance in diatoms sampled at 24 stream sites in central Western Ghats

Relation	*r*	*P*
Species composition and geographical distance	0.05	0.28
Species composition and environmental distance	0.61	0.001
Geographical distance and environmental distance	–0.05	0.53
Species composition and geographical distance with environmental distance effect controlled	0.11	0.08
Species composition and environmental distance with geographical distance effect controlled	0.62	0.002

P-values were obtained by 1000 Monte Carlo permutations.

radiation or simply due to more number of species compared to the higher organisms. The variation in matrix temperature can also be due to ecological differences between island-like systems and streams[45,46].

Furthermore, a promising and more appropriate justification for such difference in matrix temperature is related to the habitat quality and differences among sites[15,47]. Hylander *et al.*[48] have revealed that nested habitat quality has a strong influence on species pattern: high quality sites also contain more tolerant and ubiquitous species, which also occur in low quality sites. Likewise, a study on fungi[49] has shown that habitat quality was the major factor determining nestedness in substrate-specific fungi. Many of our sites have been influenced by the local water quality, which is a major determining factor of diatom assemblages. It is also important to note Allan's[50] avowal on stream ecosystem heterogeneity, that streams within a drainage system are highly connected and dynamic systems, where changes in environmental conditions occur on a temporal basis.

Species composition of diatoms in tropical streams of central Western Ghats is significantly correlated with environmental distance across geographical extent. This is seemingly in agreement with the findings of some previous studies in stream biota[51,52], in which environmental distance was identified as the key habitat feature in the structuring of stream biota assemblages. However, the relationship of diatoms with environmental and geographical variables in boreal stream seems to be different as the assemblages were related to environmental and geographical distance[14]. The disagreement is probably due to differences in the scale of investigations, as evident from the regional scope of the present study, which included a small portion in a biogeographic zone of 160,000 km^2. The current pattern suggests that at the regional level of the Western Ghats, local niche-based control influences the species composition of epilithic diatoms in streams than the effect of dispersal controls. One possible reason for variation in the diatom assemblages across sites in the same biogeographic zone is local environmental factors

Table 2. Stream water chemistry-based principal components reflecting major water quality gradients, significant variables in 24 stream sites in central Western Ghats

Principal component	PC1	PC2	PC3
Variance (%)	57.8	11.2	9.05
Significant positive correlation	Electrical conductivity (0.33), alkalinity (0.34), chlorides (0.33), calcium (0.34), sodium (0.33), potassium (0.33)	Magnesium (0.38), phosphates (0.63), nitrates (0.51)	pH (0.44), water temperature (0.55)
Significant negative correlation		Dissolved oxygen (–0.37)	Sulphates (–0.37)

such as water quality, which in turn are altered by a wide range of human activities from land-cover change to stream diversions. The Western Ghats region, like other parts of the tropics, is undergoing rapid transformation. Deforestation rate is high and forests are being transformed into agriculture and monoculture plantations. Hydroelectric projects, mining and extraction of forest products are also altering the landscape[53]. Stream biota are the first to be affected by the landscape-level changes due to contaminated run-off, which has been reported earlier through fishes[54] and aquatic invertebrates[55]. The altered quality of water could favour the wide occurrence of idiosyncratic species. Studies carried out since late 1960s on stream water quality and land-cover linkage have shown that catchment land use is a major stress on stream ecosystems, especially in agricultural regions. For example, agricultural land use in the catchment can significantly modify both water chemistry[56] and physical habitat conditions[57] that eventually decrease biological integrity in these streams[58]. Diatom community structure is believed to be strongly controlled by local environmental factors, especially water nutrient concentration and ionic composition in both tropical and temperate streams[59–62]. Heino and Muotka[41], and McAbendroth *et al.*[63] observed habitat suitability as one of the principal determinants of nestedness pattern.

Among the environmental variables analysed in this study, PCA identifies electrical conductivity, alkalinity, chlorides, calcium, sodium, potassium, magnesium, phosphates, nitrates and dissolved oxygen as the major parameters which decide the principal components. All these parameters are altered by human activities such as agriculture and organic run-off from the human settlements.

The nestedness shown by the diatom community in this study was highly significant, though it had a high proportion of idiosyncratic species, which was also noticed in earlier findings in diatoms. Idiosyncratic species were characterized with a high number of cosmopolitan species, whereas the nested species were dominated by endemic species. Mantel and partial Mantel tests showed an increase in community dissimilarity with increase in environmental dissimilarity and no relationship with geographical distance, which emphasizes the role of local environmental factors in determining the diatom species patterns. PCA identified ionic parameters and nutrients as the major features which determine the characteristics of the sampling sites. Hence the local water quality parameters are the major factors in deciding the diatom species assemblages. We conclude that landscape scale activities alter the stream local characters, which in turn decide the diatom community structure. It is also important to carry out such studies across the biogeographic zone for a larger area. This may give further insights into evolutionary patterns in the community structure of diatoms.

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