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Bioturbation functional roles associated with mangrove development in French Guiana, South America

Adélaïde Aschenbroich · Emma Michaud  · Franck Gilbert · François Fromard · Arthur Alt · Vincent Le Garrec · Isabelle Bihannic · Arnaud De Coninck · Gérard Thouzeau

Abstract This study aims to qualify, quantify, and compare the sediment reworking rates induced by the meso- (0.25–1 mm) and macro-infauna (>1 mm) along a mangrove growth gradient in the sedimentary dynamics of the French Guiana coast. The characterization of the role of small-infauna bioturbation in mangroves is new despite their known numerical dominance in tropical environments. Bare sediment, pioneer mangroves, and young mangroves were investigated during the dry season and spring tide to characterize their environment, infaunal functional community structure and sediment reworking rates. The biodiffusion differed significantly between mangrove stages, co-varying mainly with density and

functional richness. On the contrary, the non-local transport remained similar, despite the mangrove-age-specificity of infauna functional compositions, which responded to modifications in the nature and content of organic matter. The first mangrove infaunal functional sequence is described: organisms that first colonize deposited mud generate the maximum biodiffusive mixing and induce a total downward particle flux (*BDF*) as high as in the young mangroves; in the pioneer mangroves, the infauna variables and *BDF* are stressed to minimum values. Our study sheds light on the functional contribution of the small infauna in a mangrove coastal area and quantifies its role in particle transport during mangrove development.

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A. Aschenbroich · E. Michaud (✉) · A. Alt · I. Bihannic · G. Thouzeau
Laboratoire des Sciences de l'Environnement Marin (LEMAR), UMR 6539 (CNRS/IRD/UBO/Ifremer), Institut Universitaire Européen des Sciences de la mer (IUEM), Technopôle Brest-Iroise, Rue Dumont d'Urville, 29280 Plouzané, France
e-mail: emma.michaud@univ-brest.fr

F. Gilbert · F. Fromard
EcoLab, Université de Toulouse, CNRS, INPT, UPS, 31062 Toulouse, France

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V. Le Garrec
Observatoire des Sciences de la Mer et de l'Univers, CNRS, UMS 3113, Observatoire marin, Habitats benthiques, OSU-IUEM, Université de Bretagne Occidentale, Technopôle Brest-Iroise, Rue Dumont d'Urville, 29280 Plouzané, France

A. De Coninck
Centre Eau-Terre Environnement, Institut National de la Recherche Scientifique (INRS), 490 rue de la Couronne, Quebec, QC G1K 9A9, Canada

Introduction

Mangroves play a key role in the functioning of coastal ecosystems and provide ecological services and irreplaceable socio-economic value (Costanza et al., 1997). The presence of human populations living on these services is related to mangrove stability and productivity (Rezende et al., 2015). Mangroves have one of the largest annual primary productions in our biosphere (Donato et al., 2011) and organic matter (OM) degradation and mineralization provide a source of organic carbon and inorganic nutrients essential for the productivity of mangroves and the adjacent coastal waters (Bouillon et al., 2008; Alongi, 2014). Benthic biodiversity stimulates and maintains this productivity through the activities of bioturbation. This latter term is defined by “all transport processes carried out by animals that directly or indirectly affect sediment matrices. These processes include both particle reworking and burrow ventilation” (Kristensen et al., 2012). Kristensen & Alongi (2006) specifically demonstrated that the presence of oxygen due to the activity of crabs in mangrove sediments reduced the levels of sulfites, which promoted the growth of new roots of young mangroves. Such a process can have a positive effect on the growth and production of recovering mangroves (Smith et al., 2009).

In mangroves, studies evaluating the importance of bioturbation have focused on the activities of megafauna (i.e., crabs; Kristensen, 2008; Aschenbroich et al., 2016; Chen et al., 2016). However, in temperate wetlands, the bioturbation activities by small benthic invertebrates (Oligochaetes) also enhance the production of nitrogen necessary for the growth of temperate macrophytes (Mermillod-Blondin & Lemoine, 2010). As meiofauna species are highly abundant, they can markedly affect biogeochemical ecosystem functions (e.g., for nematodes: Aller & Aller, 1992; Piot et al., 2013). Alongi (1989) stated that the small-sized species dominate in tropical intertidal ecosystems because they are adapted to proportionally more recurrent constraints (e.g., freshwater inputs, massive sedimentation, climatic disturbances, etc.) compared to temperate ecosystems. Dittmann (1995, 2001) thus proposed to consider the infauna intermediate in size between the meio- and macrofauna, the so-called “mesofauna” (>0.25 mm, sensu Reise et al., 1994) in

order to deepen our knowledge about the structure and functional role of the benthic communities in tropical ecosystems.

As a primary main variable of the bioturbation process, sediment reworking is well recognized as influencing the physical structure of the sediment matrix as well as the distribution and fate of organic matter (Gilbert & Stora, 1996). Although Suzuki et al. (2012) showed that bioturbation by the small infauna promotes the subsurface transport of tracers in mangrove sediment, the quantification of biogenic sediment mixing by the small infauna in tropical areas still requires investigation (Teal et al., 2008).

According to their mode of particle mixing and transport, soft-bottom benthic organisms can be classified into five functional groups of sediment reworking: biodiffusers, gallery-diffusers, upward- and downward-conveyors, and regenerators (François et al., 1997). Their activity induces either a random particle movement over a short distance (biodiffusion) relative to the tracer's property (Meysman et al., 2003) and/or discontinuous particle transfer between the sediment surface and deeper sediment layers in a non-diffusive manner (non-local transport). The former transport is caused by biodiffusers and gallery-diffusers. The intense gallery network of the second group in subsurface sediments results in diffusive transport processes but their movements and fecal excretion at the gallery bottoms also induce non-local downward particle transport. Downward-conveyors feed at the sediment surface and transport particles non-locally to their deep egestion zone. Upward-conveyors are head-down-oriented organisms that cause particle translocation from depth (ingestion zone) to the sediment surface; surface subsidence generates a downward transport (Fisher et al., 1980). The activity of regenerators leads to particle output at the sediment surface or into the water column during digging, while burrow desertion results in passive non-local downward particle transport (Gardner et al., 1987). All these processes are constrained by mass balance, i.e., a unidirectional vector will not necessarily result in net accretion or subsidence.

The presence and intensity of biodiffusive mixing and non-local transport may vary substantially according to the structure of the benthic communities (species richness, density, biomass, and biovolume; Sandnes et al., 2000; Duport et al., 2006; Gilbert et al., 2007; Majdi et al., 2014) which in

turn depends on the environmental variables (temperature, organic matter or pollutant inputs, vegetation; Duport et al., 2007; Bernard et al., 2014; Cuny et al., 2015; Ferrando et al., 2015). Previous studies in ecology have shown that the productivity of an ecosystem is more dependent on its bioturbation functional richness than on its species richness (Solan et al., 2004; Mermillod-Blondin et al., 2005; Michaud et al., 2006; Norling et al., 2007).

In highly dynamic environments (subject to erosion, transport, and massive deposition of soft sediments), benthic communities rapidly re-colonize the sediment column: pioneer species exhibiting low species richness but high density occur in unstable sediments, whereas high species richness and low density represents more stable sediments (Rhoads & Germano, 1986; Aller, 1989; Michaud et al., 2003). Does low taxonomic diversity in such dynamic environments automatically result in low sediment reworking? This question will be addressed in this study, in the early stages of the mangroves in French Guiana, which have specific dynamics compared to other mangroves in the world. The Guianese coast is indeed a unique entity, subjected to successive phases of massive suspended sediment discharge from the Amazon River and sediment erosion (Anthony et al., 2010). Mangrove dynamics follow the newly formed mud banks along the coast, with mangroves colonizing rapidly as soon as the mud is sufficiently consolidated (Fromard et al., 2004; Proisy et al., 2009). Mud deposition and subsequent mangrove development thus involve significant benthic habitat modifications through vegetation and sediment structuring (Fromard et al., 1998; Marchand et al., 2003; Aller et al., 2004). The first data acquired on the Guianese mud banks indicated that the benthic system is adapted to these phases of stability and instability (Aller & Stupakoff, 1996; Dupuy et al., 2015) but the role of the benthic diversity of the small infauna through its bioturbation activities in French Guiana mangroves is still unknown.

This study characterized, at the mouth of the Sinnamary estuary (French Guiana) during the dry season and the spring-tide period, (1) the modifications of the taxonomical and functional structures of the benthic communities of meso- and macro-infauna along a mangrove growth gradient, (2) the modes and rates of sediment reworking, and (3) their relationship to the infaunal variables (taxonomic and functional

richness, density, biovolume) in the littoral mangrove of Sinnamary.

Materials and methods

Study area

The study was carried out in a mangrove area colonizing the intertidal part of the mud bank located north-west of the Sinnamary estuary in French Guiana (5°28'41"N, 53°02'05"W; Fig. 1A). Following the bare sediment accretion and elevation processes, the consolidated mud bank in this study site was colonized in early 2012. The development of the pioneer mangroves led to the establishment of a fringe of young mangroves. Consequently, early stages of mangrove development (hereafter referred to as "sites": bare sediment, pioneer mangroves and young mangroves) were identified in the area and corresponded to a vegetation development profile along the intertidal gradient (Fig. 1B). It is important to note that the mud sediment topography over which the forest develops parallel to the shoreline is very smooth (1:2000; Gardel & Gratiot, 2005). Pioneer and young mangroves grow on a sedimentary bed whose elevation varies slightly from 2.6 to 2.8 m and 2.7 to 2.95 m, respectively, above the hydrographic zero which is defined as the level of the lowest astronomical tides (Proisy et al., 2009). The tide is semidiurnal with spring and neap high-tide water levels up to 3.2 and 2.8 m, respectively. The spring tidal range is 2.1 ± 0.3 m, whereas the neap tidal range is 1.3 ± 0.3 m. The three study sites were thus fully inundated during spring high tides but the pioneer and young mangroves were not inundated for 4–5 consecutive days during neap high tides (Proisy et al., 2009). However, differences in substrate elevation between sites induce a difference in emersion/immersion time between the bare sediments and the vegetalized sediments. The emersion time lasts ca. 5h00 in the bare sediments, ca. 7h30 in the pioneer mangroves, and ca. 8h00 in the young mangroves over a tidal period of 12h15 (field observations). Those values may vary, however, with the topographic elevation level, within each site, along the study area. This approximately represents emersion/immersion time frequencies of 40%/60%, 60%/40%, and 65%/35% of the total tidal duration, for the bare sediments, the pioneer, and young mangroves, respectively.

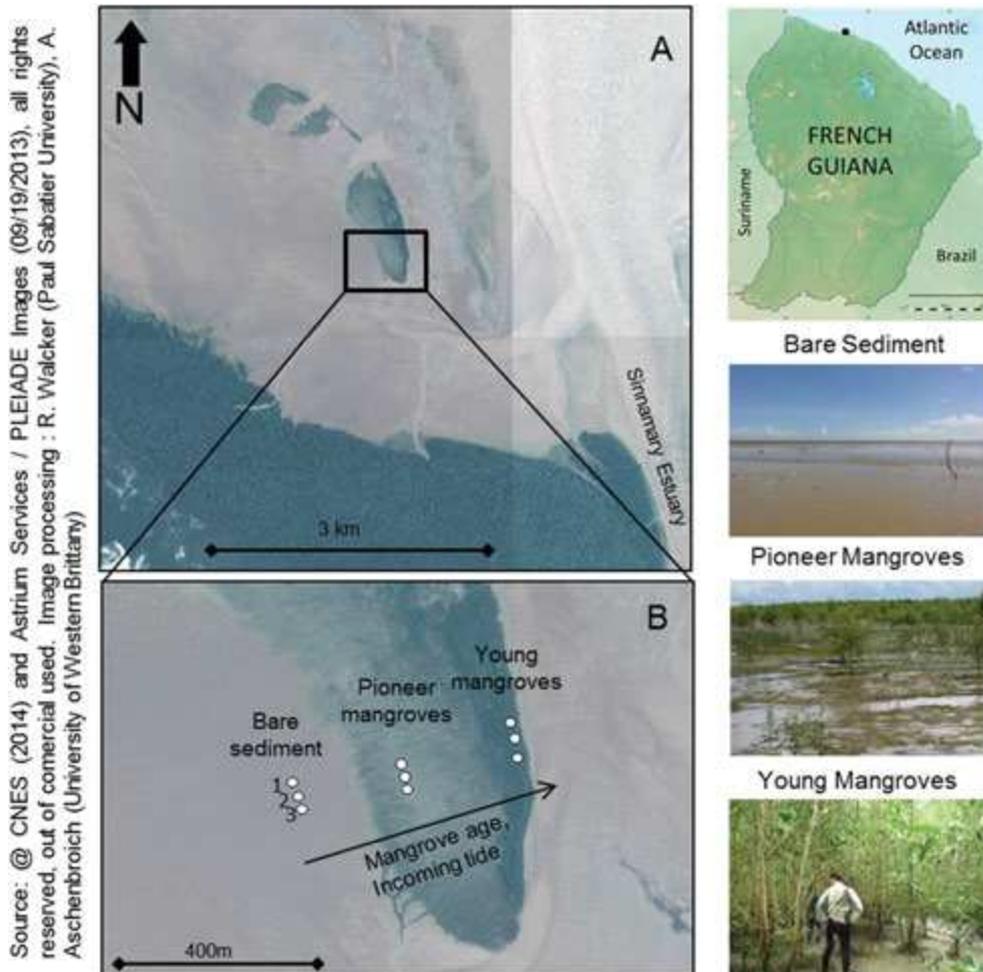


Fig. 1 A Study area located north-west of the Sinnamary estuary in French Guiana. B Locations of the three stations (1, 2, and 3; *white dots*) sampled within each stage of mangrove development (sites: bare sediment, pioneer mangroves, and young mangroves *cf.* pictures on the *right*). Stations within a

same site are 25 m apart. Source: @ CNES (2014) and Astrium Services / PLEIADE Images (09/19/2013), all rights reserved, out of commercial use. Image processing : R. Walcker (Paul Sabatier University), A. Aschenbroich (University of Western Brittany)

Each stage of mangrove development was investigated between October 10 and 14, 2013 during the spring tide. Due to site accessibility constraints, the study sites were reached during the rising spring tides between 11:00 am and 2:00 pm. In situ water temperature, salinity, and oxygen saturation at high tide were previously recorded at each study site using commercially available YSI 6920v2 probes (YSI Inc., Yellow Springs, OH, USA), which indicated homogeneous values across the three study sites ($28.3 \pm 1.2^\circ\text{C}$; 7.4 ± 0.6 psu; $75.68 \pm 4.83\%$ oxygen saturation). At each study site, three stations were GPS marked, referred to as station 1, station 2, and

station 3, and investigated for vegetation, sediment, fauna, and bioturbation sampling, making a total of nine stations for the entire study area. The same distance (25 m) separated two successive stations at each study site (Fig. 1). Since the three stations of each study site were placed parallel to the shoreline, they were subjected to the same tidal level at the same time.

Structure of the mangrove vegetation

Sites were investigated at low tide in order to describe the vegetation structure of each stage of mangrove development. Tree identification, height, and density

were studied within plots whose number and surface area were adapted to stem density (Fromard et al., 2004): a large plot area of 27,500 m² covering the three stations (1, 2, 3) with bare sediment; one plot of 400 m² per station at the pioneer mangrove site; and three 1 m² plots per station at the young mangrove site. The number of pneumatophores was also counted and converted into density in order to estimate the spatial complexity structure imposed by the vegetation on the benthic compartment, and the mangrove litter was collected to evaluate its biomass.

Sedimentary characteristics

In order to characterize and relate the sedimentary habitat to the infauna community structure at each stage of mangrove development, the sediment dry density, total particulate carbon and nitrogen, and the quantity of available benthic phyto-material were measured in the sedimentary column within 10 m of each GPS-marked station. One sediment core (Plexiglas tube, 10.4 cm diameter, 18 cm height, 84.9 cm² area) per station was collected from a kayak during high tides (Fig. 2). Cores were sliced into 0.5-cm layers from 0 to 5 cm depth, 1-cm layers from 5 to 10 cm depth, and 2-cm layers from 10 to 18 cm depth. Sedimentary parameters obtained for all homogenized slices were averaged per core to overcome the effect of the tidal cycle variability on such parameters.

Dry bulk sediment density (δ) was determined for each sample by drying and weighing (m) a known

volume (V) of sediment ($\delta = m/V$). The remaining sediment was frozen for subsequent analysis of photosynthetic pigments, organic carbon and nitrogen, as well as grain size. Pigments were determined by adapting the methods of Lorenzen (1966), Riaux-Gobin & Klein (1993) and Buffan-Dubau & Carman (2000): Chl-*a* was extracted in 90% acetone for 18 h from freeze-dried sediments. Concentrations were determined fluorometrically on a Turner 10-AU fluorometer (Turner design, San Jose, CA, USA), using an acidification step to separate phaeopigments from chlorophyll *a* pigments. Total carbon and nitrogen were analyzed by combustion at 930°C on a CHN analyzer (FLASH-2000; Thermo Fisher Scientific Inc., Milan, Italy). Marchand et al. (2003) previously qualified and quantified the sediment organic matter of the Sinnamary coastal area. The authors showed that, due to the lack of carbonates, the organic fractions largely dominated or equally corresponded to the total carbon. The total carbon and nitrogen were thus used as proxies of the organic matter, and the associated C:N ratio (mol:mol) was calculated in order to evaluate the refractory versus labile nature of the sediment organic matter. Grain size dependence on depth was previously analyzed in sediment cores sampled in 2012 at the same study sites. The preliminary results showed that the median grain size was homogeneous over depth in bare sediments and mangroves facies (median grain size range and mean were 5.1–6.8 μ m and $5.9 \pm 0.5 \mu$ m, respectively), as also suggested by previous works (Allison et al., 2000; Debenay et al., 2007). In the

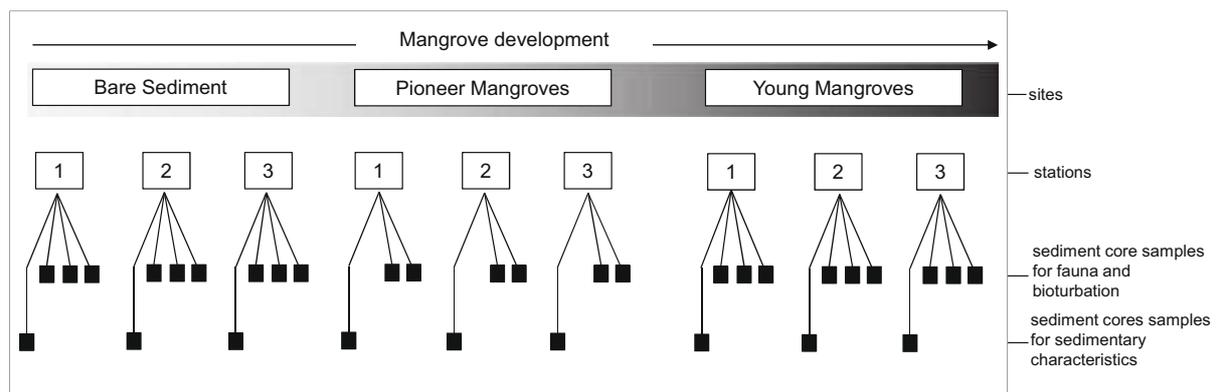


Fig. 2 Study design employed for the statistical study of the changes in the biologically induced sediment reworking in relation to the meso- and macrofauna community structure and

the sediment characteristics along a mangrove development gradient crossing bare sediment, pioneer, and young mangroves

current study, median grain size was thus analyzed only in the surface sediments sampled at each station, using a Malvern Mastersizer S2000 (Malvern Instruments Ltd, Malvern, UK). Prior to measurement, organic matter was removed and aggregated particles were deflocculated following Sperazza et al. (2004).

Bioturbation measurement and infauna collection

Additional sediment cores (10.4 cm diameter, 18 cm height, and 84.9 cm² total area) were collected at each station for bioturbation measurement and infauna collection. Triplicate sediment cores were initially sampled at each station at the three sites, but three cores from the pioneer mangrove site were accidentally lost, leading to a total of six sediment cores at the pioneer mangrove site ($n = 6$) and nine sediment cores at the bare sediment ($n = 9$) and young mangrove ($n = 9$) sites. The cores were kept intact and undisturbed during the first 24 h for sediment stabilization and faunal acclimation. They were then incubated ex situ in seawater-filled tanks (as in Dupont et al., 2007; Cuny et al., 2015) outside, under natural light, thus respecting the light/night cycle. The cores enclosed a volume of overlying water of ca. 849 cm³. Since no seawater circulation system could be implemented, the overlying water of each core was renewed manually (Michaud et al., 2010). Since we were not able to mimic accurately the emersion/immersion frequency for each stage of mangrove development due to logistic constraints, a similar tidal cycle of 6 h:6 h was applied to the whole set of cores, representing an immersion/emersion frequency of 50%/50% over a total tidal duration of 12 h. Although the emersion/immersion duration specific to each site was not accurately mimicked in our study, this represented a deviation of ± 20 –30% of the real tidal cycle for each mangrove facies. In the frame of this pioneer study, we nevertheless assumed this allowed meaningful comparison of bioturbation results between cores. The overlying water of each core was left for 6 h to mimic the high tide. During this time, the overlying water of each core was gently mixed and oxygenated by an individual aerator, thus avoiding dissolved oxygen under saturation. To mimic the low tide, the overlying waters were then removed and the low tide lasted 6 h. New fresh seawater from the study area was sampled everyday to renew the overlying water of each core. No specific probe was

implemented in the seawater-filled tanks but probes were used to measure the new fresh seawater added in the tanks (cf ‘study site’).

In order to quantify the biologically induced sediment transport in cores, inert fluorescent particles, referred to as microspheres hereafter (Fluoresbrite[®] YG Microspheres, Polysciences Europe GmbH, Eppelheim, Germany), whose diameter (10 μm) corresponded to in situ silt sediment grains (70% of grains: $4 < x < 31 \mu\text{m}$; preliminary data of 2012), were homogeneously introduced into a mud layer and deposited at the core sediment surface (Gerino et al., 2007; Lagauzere et al., 2011). The mud layers (2 mm thick, 10.4 cm diameter) were prepared with a mixture of surface sediment from each station and 400 μl of microsphere. Cores were incubated for 10 days, which is the minimum time to enable the characterization of the different transport modes. Incubation time that exceeds 10 days increases the probability of complete homogenization of the sedimentary column, and may thus prevent the differentiation of transport modes (François et al., 1997). After ten days, the sediment cores were sliced into 0.5-cm layers from 0 to 5 cm depth, 1-cm layers from 5 to 10 cm depth, and 2-cm layers from 10 to 18 cm depth. Each slice was carefully homogenized and 3 cm³ subsamples were removed for microsphere quantification. The remaining sediment was sieved through 1-mm and 0.25-mm meshes to collect the macrofauna ($x > 1 \text{ mm}$) and mesofauna ($0.25 < x < 1 \text{ mm}$), respectively. The latter was fixed in 4% buffered formaldehyde and stored in a 70% ethanol solution until identification.

Sediment reworking quantification

In order to evaluate the vertical microsphere distribution in cores, the homogenized subsamples of each sediment slice were deposited in 25-well microplates. The proportions of microspheres were quantified by fluorescence (bottom reading fluorescence; λ excitation = 441 nm; λ emission = 486 nm; number of readings per well: 9×9) using a microplate reader Sinergy Mx (BioTek Instruments Inc., Winooski, VT, USA) following Lagauzere et al. (2011) and Majdi et al. (2014). Fluorescence values resulting from the microsphere emissions were obtained by subtracting the fluorescence value of natural sediments at different depths (additional cores) from the fluorescence measurements of incubated sediments. Results were

converted into percentages of total microspheres initially deposited at the sediment surface.

Given that sediment was removed from a surface sediment marked layer with a thickness e_i of 0.2 cm, a surface area S of 84.99 cm², a volume $V = S \times e_i = 16.99$ cm³, and knowing the surface sediment dry density δ (g_{dw} cm⁻³) of each mangrove stand, the proportion of microspheres that have been buried B (%), and the incubation time Δt (year), the biological downward particle flux from the surface (BDF g cm⁻² year⁻¹) was expressed as $BDF = \frac{B}{\Delta t} \times \frac{V}{S} \times \delta$.

In order to identify, quantify, and compare the tracer transport modes biologically induced for each stage of mangrove development, the gallery-diffusor model of François et al. (2002), revised in Dupont et al. (2007), was used in this study. This model quantifies both biodiffusion-like transport (Db coefficient; cm² - year⁻¹) and the non-local transport of the tracers (r coefficient; year⁻¹) in universal metrics. It adjusts a theoretical curve of the tracer distribution with depth on experimental data. The best fit between the observed and modeled tracer distribution is estimated by the least squares method and produces the best Db and r coefficient couple.

Description of the infauna community structure

The infauna from cores was identified at the lowest practical taxonomic level to estimate the taxa richness (number of taxa). Image-based measurements of organism length and width (Visilog[®] software, Noesis, France, 1 px equal to 1.0–12.4 μm according to the magnification used) taken under a binocular microscope were converted into biovolume (ml) by relating organisms to geometrical forms: cylinders (e.g., Nematodes and Annelids, i.e., $\pi r^2 h$) and ellipsoids (e.g., Ostracods, Copepods, and Bivalves, i.e., $\frac{4}{3} \pi r_x r_y r_z$). This method is widely used for the study of meiofauna taxa (i.e., Copepods, Nematodes; Zepilli et al., 2014). It was applied to the smallest individuals in this study. The biovolume of larger individuals (>10 mm) was directly obtained by immersing the organisms in graduated filled containers (Michaud et al., 2005).

There are several functional categorizations, which include one or more species traits such as mobility, trophic mode, or sediment reworking mode/intensity, whose identification is constrained by the information

available on species (Törnroos & Bonsdorff, 2012; Queirós et al., 2013). Because organism size and type of sediment transport determine their impact on ecosystem functioning (e.g., Biles et al., 2002; Gilbert et al., 2007; Norkko et al., 2013), both of these traits were combined to create functional groups (FG) in this study. Invertebrates were referred to as either mesofauna (0.25 < x < 1 mm) or macrofauna (>1 mm) and as biodiffusors (B), conveyors (C), gallery-diffusors (GD), regenerators (R) or unknown (U) using the information available from the literature (Online Appendix 1). Since this study cannot distinguish upward and downward transport, the general conveyor mode was used. Taxa that could not be identified at species level or species whose behavior is not described in the literature were categorized by (i) assuming behavior fit to one of a taxonomically close species, or (ii) theorizing the type of mixing induced from their burrowing behavior. The functional richness in cores was subsequently assessed as the number of functional groups.

Organism density and biovolume were evaluated per taxon, functional group, and in total for each sediment core, and subsequently converted per square meter (area) in order to provide relevant surface values. The biovolume to abundance (Bv:A) ratio was calculated per core as a proxy of the mean organism size.

Data analysis

Univariate analysis

Differences in sedimentary characteristics, infaunal community, and bioturbation variables between sites (bare sediment, pioneer mangroves, and young mangroves) were explored by analysis of variances. To satisfy homoscedasticity and normality requirements, *Chl-a* and *Db* were $\log(x + 1)$ transformed. Parametric analyses (ANOVA) and pairwise comparison tests (Tukey's HSD Post hoc) were then applied to these variables. Differences in C:N ratio, community density and biovolume (total, mesofaunal, macrofaunal, and per functional group, i.e., size \times sediment reworking groups), functional richness, and the biovolume to abundance ratio (Bv:A) between sites were tested using the non-parametric analysis of variances (Kruskal–Wallis test) followed by the Wilcoxon pairwise comparison test, due to the non-homoscedasticity of the data.

Multivariate analysis

A non-parametric permutational multivariate analysis of variance (PERMANOVA; Anderson, 2001) based on matrix of density and biovolume per functional group was computed to test the multivariate response of infauna assemblages to the stage of mangrove development (bare sediment, pioneer mangroves, and young mangroves) after verifying the multivariate homogeneity of group dispersions. A co-inertia analysis was performed to visualize the contribution of the infauna functional composition and the depth-averaged sediment environmental variables to the discrimination of stations according to stages of mangrove development. The former ordinated stations according to both their fauna and environmental characteristics, when the datasets have different numbers of environmental variables, species, and/or samples (Doledec & Chessel, 1994). The relatedness of the two datasets was measured by the multivariate coefficient of correlation (RV). The infauna matrix corresponds to the abundances of each functional group (size \times sediment reworking), which were summed per station. For multidimensional analyses, faunal data were first Hellinger transformed to avoid bias towards rare species (Legendre & Gallagher, 2001).

Correlation analysis

Correlation analyses were used to quantify the relatedness between sediment variables and functional groups, and to explore whether the sediment reworking rates (Db , r , BDF) were significantly and positively associated with (1) the infauna density, biovolume, taxa, and functional richness, and (2) the density or biovolume of each functional group (size trait, sediment reworking trait, interaction of size \times sediment reworking traits), which could drive the rates. All relationships were tested with either the parametric Pearson or the non-parametric Spearman multi-correlation analysis after data normality verification. The correlation coefficients (r for Pearson, referred to as r_p hereafter to avoid confusion with the non-local transport coefficient, and ρ for Spearman) quantify the statistical dependency between variables, i.e., the strength of the correlation.

Results

Description of the three stages of mangrove development

The bare sediment lacked vegetation, whereas the pioneer and young mangroves were dominated by *Avicennia germinans* (>80%). The bare sediment thus represents an initial time before mangrove establishment. In the pioneer mangroves, mean tree height was 0.24 ± 0.02 m (mean \pm SD) and their distribution was sparse (208.3 ± 62.9 ind ha^{-1}) (Fig. 3). In the young mangroves, mean tree height and density were 4.12 ± 2.26 m and $92,222.2 \pm 29,907.3$ ind ha^{-1} , respectively. The pneumatophore density and the litter biomass increased with mangrove growth, being significantly higher in the young mangroves (340.3 ± 201.2 pneumatophore m^{-2} , litter = 2.8 ± 1.1 $g_{dw} m^{-2}$) than in the pioneer mangroves ($\leq 0.06 \pm 0.02$ pneumatophores m^{-2} ; Kruskal–Wallis, $P < 0.05$).

Surface sediment characteristics

Table 1 shows the significant differences in all sedimentary variables between sites except for the median grain size (ANOVA, $P > 0.05$). The dry sediment density slightly but significantly decreased in the young mangroves (ANOVA, $P < 0.05$). Total carbon (TC) exhibited a significant decrease from the

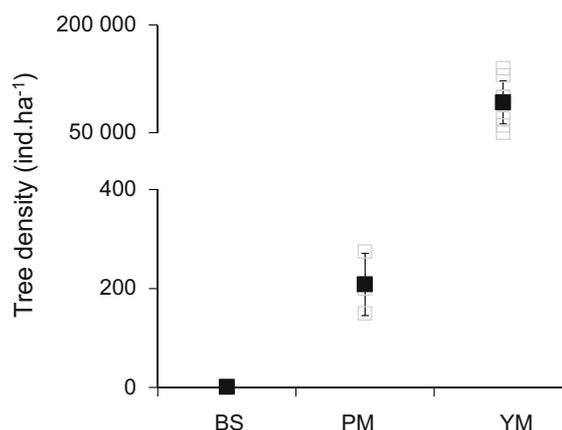


Fig. 3 Changes in mangrove tree density between stages of mangrove development. *Black-filled* and *gray-open* symbols represent mean (\pm SD) and replicate values, respectively. *BS* bare sediment, *PM* pioneer mangroves, *YM* young mangroves

bare sediment to the young mangroves (ANOVA, $P < 0.001$), whereas total nitrogen (TN) content and Chl-*a* concentrations significantly increased in the pioneer mangroves (ANOVA, $P < 0.001$). Consequently, the C:N ratio was the lowest in the pioneer mangroves (Kruskal–Wallis, $P < 0.05$).

Infauna community structure

The total density and biovolume of the benthic community ranged from 1,413 to 142,204 ind m^{-2} and from 0.1 to 117.3 ml m^{-2} , respectively (Fig. 4, Online Appendix 1). Total, mesofaunal, and macrofaunal densities were significantly higher in the bare sediment (Wilcoxon, $P < 0.01$; Fig. 4A). Total and macrofauna biovolumes significantly decreased in the pioneer mangroves (Wilcoxon, $P < 0.01$, Fig. 4B), whereas mesofaunal biovolumes were similar between the pioneer and young mangroves and significantly higher in the bare sediment (Wilcoxon, $P < 0.01$, Fig. 4B). The biovolume-to-abundance ratio, taxa and functional richnesses significantly decreased in the pioneer mangroves (Online Appendix 1).

Seven of the eight functional groups defined (4 modes of sediment mixing \times 2 size classes) were identified in the study area (Online Appendix 1). The taxa that could not be associated with a mode of sediment reworking were referred to as ‘unknown’. This group represented less than 1.7% of the total density and biovolume of the infauna community; thus, this group of unknowns was not represented in the results. The density and biovolume of the gallery-diffusors and biodiffusors varied significantly among stages of mangrove development (Fig. 4;

Kruskal–Wallis, $P < 0.05$), whereas the biovolume of conveyors was similar between sites (Fig. 4B). Specifically, the density and biovolume of the meso-conveyors, meso-biodiffusors, and gallery-diffusors were highest at the bare sediment site. For the meso-conveyors, these variables decreased significantly and gradually with mangrove growth (Kruskal–Wallis, $P < 0.05$ for all; Fig. 4).

Sedimentary characteristics versus infauna relationships

Figure 5 summarizes station discrimination between stages of mangrove development according to their functional composition and sedimentary characteristics. Both matrices were correlated at $RV = 0.7$. The two first axes explained 99% of the total variance. The first axis mainly differentiated the bare sediment from the pioneer mangroves. It opposed the labile material (Chl-*a*, TN) in pioneer mangrove sediments to the increasing C:N ratio and the median grain size in the bare sediment in relation to the increasing contribution of the meso- and macro-gallery-diffusors to the infauna community. The second axis only slightly explained station variances (6.6%). The analysis of the multivariate responses of the infauna communities (density and biovolume per functional group or taxon) confirmed the site specificity of infauna assemblages (PERMANOVA analysis; density: $P < 0.001$; biovolume: $P < 0.05$).

Correlation analyses quantified the statistical dependency between the infauna community variables and depth-averaged sedimentary characteristics

Table 1 Depth-averaged sediment characteristics from core samples (mean \pm SD, H = 18 cm) in the three sites (*BS* bare sediment, *PM* pioneer mangroves and *YM* young mangroves) sampled in October 2013 and surface sediment median grain size

	Bare sediment (BS)	Pioneer mangroves (PM)	Young mangroves (YM)	Differences between sites		
				Test	<i>P</i>	Pairwise comparisons
Sediment density ($g_{dw} cm^{-3}$)	0.75 \pm 0.01	0.72 \pm 0.02	0.64 \pm 0.05	A	*	BS \neq YM
TN (%)	0.13 \pm 0.00	0.15 \pm 0.00	0.13 \pm 0.00	A	***	BS \neq PM \neq YM
TC (%)	1.19 \pm 0.03	1.10 \pm 0.01	0.96 \pm 0.04	A	***	BS \neq PM \neq YM
C:N	10.25 \pm 0.14	8.58 \pm 0.04	8.94 \pm 0.11	KW	*	BS \neq PM \neq YM
Chl- <i>a</i> ($\mu g \cdot g^{-1}$)	2.08 \pm 0.25	12.47 \pm 1.98	2.19 \pm 0.59	A	***	PM \neq
Median grain size (μm)	7.72 \pm 0.85	6.21 \pm 0.26	7.06 \pm 0.49	A	ns	

Differences in the variables between sites after one-way ANOVAs (A) or Kruskal–Wallis (KW) tests: * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$, ns: non-significant. The pairwise comparison denotes significantly different sites. Analysis was done on $\log(\text{Chl-}a + 1)$

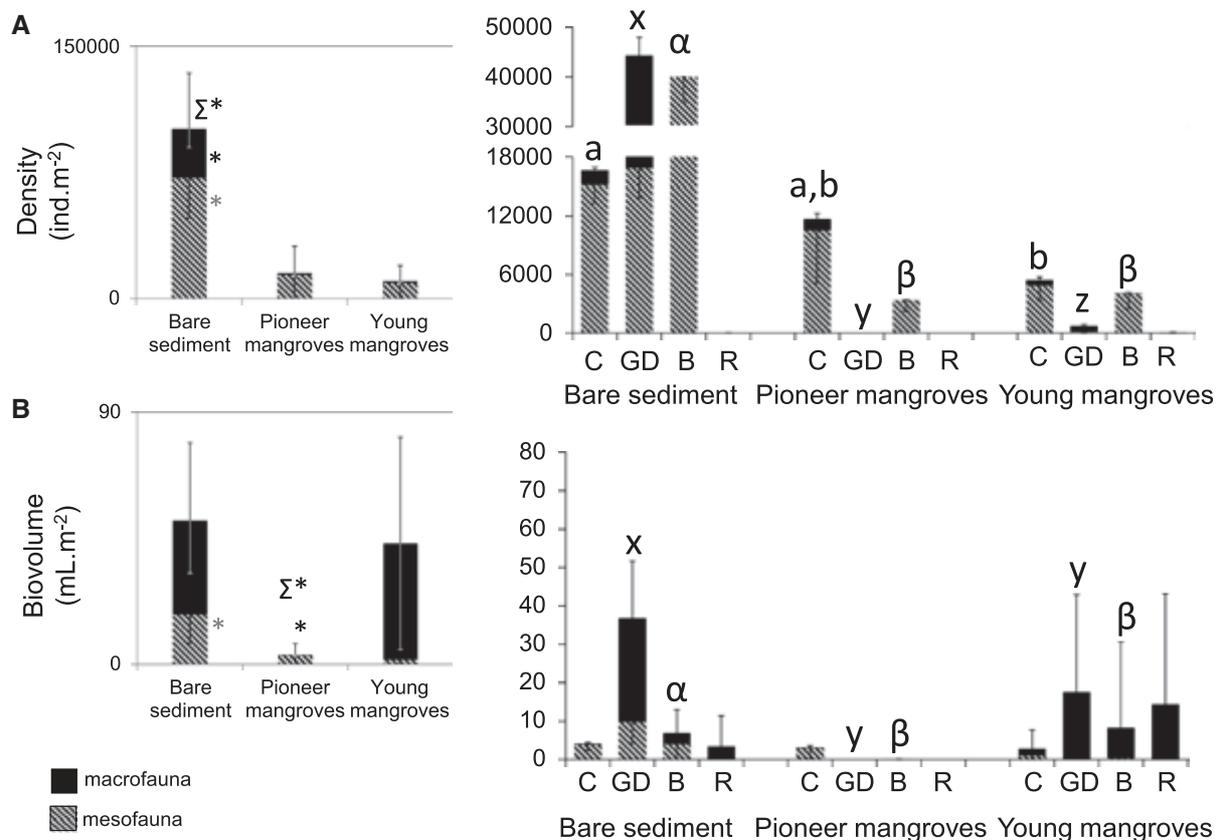


Fig. 4 Changes in density and biovolume of the infauna community between stages of mangrove development. *Left panels:* mean **A** density and **B** biovolume of the total macrofauna (black, -SD), total mesofauna (crossed, -SD), and total community (+SD) per stage of mangrove development. Σ^* , black, and gray asterisks mark the significant differences in total, macrofaunal, and mesofaunal density and biovolume, respectively, between stages of mangrove development. *Right panels* represent the mean (+SD) **A** density and

B biovolume of functional groups (mesofauna: *crossed bars*, macrofauna: *black bars*, C: conveyors, GD: gallery-diffusor, B: biodiffusors, R: regenerators) according to the mangrove stage; the significant differences in a given functional group between stages are denoted by letter changes between (a, b) for conveyors, (x, y, z) for gallery-diffusors, and (α , β) for biodiffusors. The density and biovolume of the other functional groups are not significantly different between stages of mangrove development

(Table 2). The mean organism size revealed by the biovolume-to-abundance ratio (Bv:A), was inversely correlated to the labile organic matter expressed by TN content and Chl-*a* concentrations, which were maximum in the pioneer mangroves. The total density and biovolume of the community increased as a function of TC, C:N, and median grain size. Results related the macro-conveyor densities to the sediment TC. A strong correlation linked the density and biovolume of the meso- and macro- gallery-diffusors with the C:N ratio and median grain size, and the meso-biodiffusors with the C:N ratio. The density and biovolume of the macro-biodiffusors decreased as a function of increasing Chl-*a* concentration.

Microsphere vertical distribution

The burying of tracers below the surface was noticeable at all three mangrove stages (Fig. 6). Microspheres were buried up to 18 cm but were mostly observed in the first 2 cm. Microsphere percentages showed an exponential decrease in the subsurface sediments, expressing a biodiffusive particle mixing until ca. 2, 0.75, and 1.75 cm in bare sediment, pioneer, and young mangroves, respectively. In the bare sediment and pioneer mangroves, tracers were frequently transported to several depths between 3 and 11 cm below the surface, whereas in young mangroves non-local transport occurred mostly above

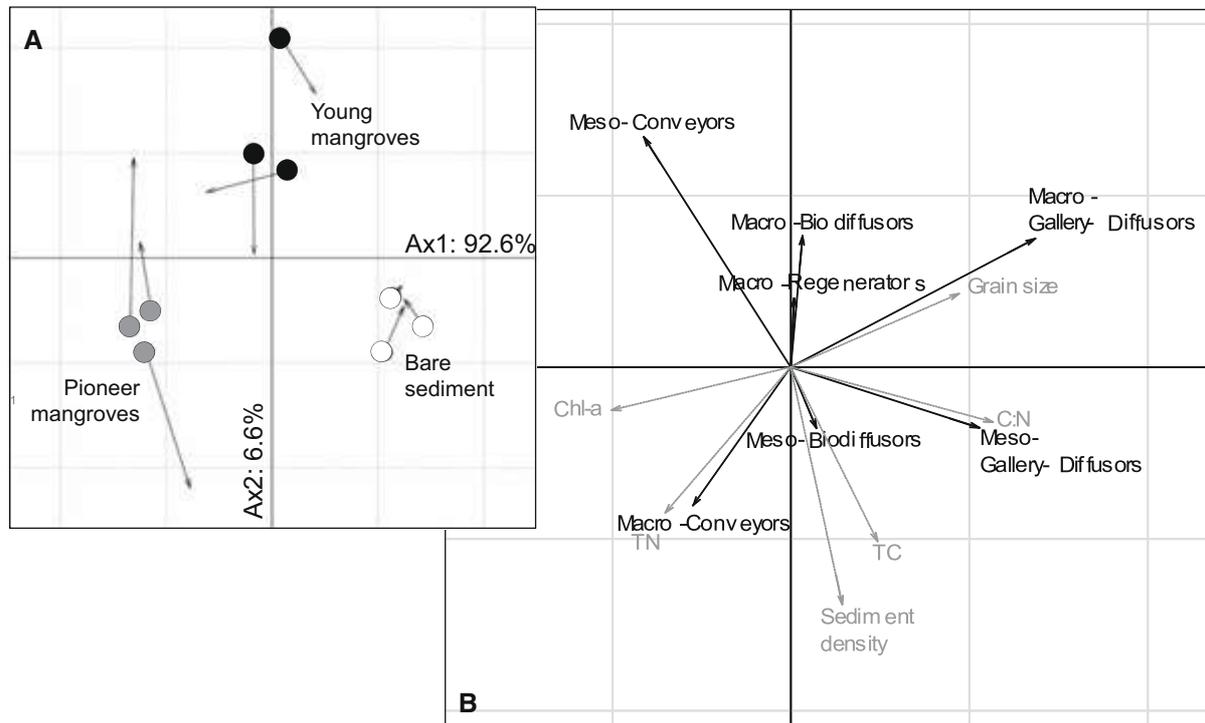


Fig. 5 Co-inertia analysis of 6 sedimentary variables averaged over 18-cm depth and the density of 7 functional groups of bioturbation from 9 stations investigated in the three stages of mangrove development (bare sediment, pioneer mangroves, and young mangroves). **A** Ordination of stations on the co-inertia axes, using environmental variables (origin of the *arrows*) and community functional composition (*arrowheads*) co-inertia

8 cm depth. Tracers in cores from the pioneer mangroves were sometimes not buried ($n = 2$) resulting in a higher microsphere proportion in the first 2 cm than at other sites (Wilcoxon, $P < 0.001$). Below 5 cm, higher proportions of microspheres were buried in bare sediment than at other stages of mangrove development (Wilcoxon, $P < 0.01$) while tracer proportions were similar between the pioneer and young mangroves at these depths.

Sediment reworking modes and intensity

Sediment reworking rates are given in Table 3. The biodiffusion coefficients Db ranged from 0 to $9.1 \text{ cm}^2 \text{ year}^{-1}$ over the study area; mean values were significantly higher in the bare sediment ($5.48 \text{ cm}^2 \text{ year}^{-1}$) than in the young mangroves ($1.69 \text{ cm}^2 \text{ year}^{-1}$) and pioneer mangroves ($0.21 \text{ cm}^2 \text{ year}^{-1}$). The non-local transport r coefficients ranged from 0 to 21 year^{-1} over the study area. The mean r slightly

weights. **B** Contributions of the community composition (based on Hellinger-transformed abundance data; *black arrows*) and environmental variables to the canonical space (*gray arrows*, code given below). Grain size: median grain size, Chl-*a*: Chlorophyll-*a*, *TN* total nitrogen, Sediment density: dry sediment density, *TC* total carbon, *C:N* carbon-to-nitrogen ratio

decreased from the bare sediment to the young mangroves (from 5.52 ± 4.7 to $3.69 \pm 6.87 \text{ year}^{-1}$). Both types of transport resulted in a BDF ranging from 0 to $2.8 \text{ g}_{\text{dw}} \text{ cm}^{-2} \text{ year}^{-1}$ over the study area with significantly higher values in the bare sediment and young mangroves (Table 3).

Relationships between infauna and sediment reworking rates

The relationships between the sediment reworking rates and the taxa and functional richnesses are detailed in Table 4. BDF and Db significantly increased with functional richness and total taxa densities. However, the communities composed of 3, 5, and 6 functional groups resulted in variable BDF and Db rates (Fig. 7). Only Db linearly increased with the biovolume of the community. The non-local transport coefficient r did not show any apparent link with the total primary community variables (Table 4).

Table 2 Spearman's rank and Pearson correlations between depth-averaged sediment characteristics and the total density (D), biovolume (Bv) and biovolume-to-abundance ratio (Bv:A), or the density and biovolume of a given functional group

	Total community variables			Functional groups													
	D	Bv	Bv:A	Meso-C		Macro-C		Meso-GD		Macro-GD		Meso-B		Macro-B		Macro-R	
				D	Bv	D	Bv	D	Bv	D	Bv	D	Bv	D	Bv	D	Bv
Sediment density ($\text{g}_{\text{dw}} \text{cm}^{-3}$)	ns	ns	ns	ns	ns	0.60	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
TN (%)	ns	-0.70 ^P	-0.83**	ns	ns	ns	ns	ns	ns	ns	-0.60 ^P	ns	ns	ns	ns	ns	ns
TC (%)	0.75*	ns	ns	0.64 ^P	0.68 ^P	0.70* _p	ns	ns	ns	ns	ns	0.75*	0.61	ns	ns	ns	ns
C:N ratio	0.80**	0.73*	ns	0.64	0.64	0.65	ns	0.76*	0.78*	0.86**	0.71*	0.80**	0.89***	0.83**	0.66	0.59	ns
Chl- <i>a</i> ($\mu\text{g}\cdot\text{g}^{-1}$)	ns	ns	-0.73*	ns	ns	ns	ns	-0.68*	-0.64	-0.66	-0.74*	ns	ns	-0.80**	-0.83**	ns	ns
Median grain size (μm)	0.67*	0.81*** ^P	ns	ns	ns	ns	ns	0.82**	0.76*	0.93***	0.93*** ^P	0.67*	0.76*	ns	ns	ns	ns

The correlation coefficients ρ (non-parametric Spearman) and r_p (parametric Pearson, denoted by ^P) are given when probability was $p < 0.1$. Significance of the correlation: * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; ns non-significant at $p \geq 0.1$

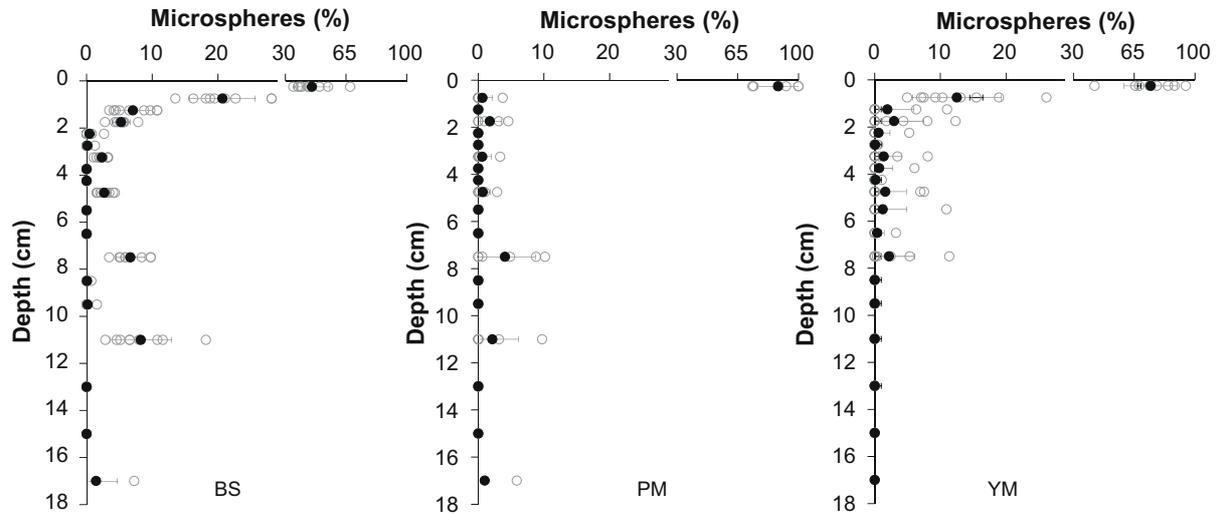


Fig. 6 Depth profiles of microsphere tracers (%) at all three stages of mangrove development (*BS* bare sediment, $n = 9$; *PM* pioneer mangroves, $n = 6$; *YM* young mangroves,

$n = 9$). *Black-filled* and *gray-open circles* represent means (\pm SD) and replicate values, respectively

Table 3 Mean (\pm SD) sediment reworking coefficients (Db , r) and BDF at *BS* bare sediment, *PM* pioneer mangroves, and *YM* young mangroves

Stage of mangrove development	Db ($\text{cm}^2 \text{ year}^{-1}$)	r (year^{-1})	BDF ($\text{g}_{\text{dw}} \cdot \text{cm}^{-2} \text{ year}^{-1}$)
BM	5.48 ± 2.52	5.52 ± 4.7	1.51 ± 0.3
PM	0.21 ± 0.35	4.46 ± 4.79	0.48 ± 0.5
YM	1.69 ± 0.88	3.69 ± 6.87	1.23 ± 0.7
<i>Effect</i>			
df	2	2	2
F ratio	44.29	0.237	6.512
P	<0.001	0.791	<0.01
<i>Multiple-comparison</i>			
BS	a	a	a
PM	b	a	b
YM	c	a	a

The effect of the stage of mangrove development on $\log(Db + 1)$, r and BDF (ANOVA) and multiple comparisons (Tukey's HSD). Db biodiffusion coefficient; r non-local transport coefficient; BDF total biological downward particle flux; df degrees of freedom; P probability. For multiple comparisons, bold letters highlight the significant difference of the mangrove stage from others (significance level at $\alpha = 0.05$)

More specifically, Db increased as a function of the density and biovolume of the gallery-diffusers (Amphipoda sp. 1 and the Tanaids *Discapseudes surinamensis* and *Halmyrapseudes spaansi*) and the meso-biodiffusers (Nematoda spp. and Ostracoda sp.; Table 4). The non-local transport increased together with the macrofauna density and the meso-conveyor biovolume (mainly Oligochaeta spp.; Table 4). The

BDF was correlated to the density and biovolume of the total macrofauna, the gallery-diffusers (notably the Amphipods and Tanaids), and the meso-biodiffusers (mainly Nematoda spp.; Table 4).

Relationships between infauna and sediment reworking showed environmental specificity. In the bare sediment and pioneer mangroves, the non-local transport increased with the density of the macro-

Table 4 Spearman's rank ρ and Pearson r_p (^P) correlations coefficients ($n = 24$) of the sediment reworking rates (*Db*: biodiffusion, *r*: non-local transport, *BDF*: biological downward

particle) with the total infauna variable or with the density (D) and biovolume (Bv) of the mesofauna, macrofauna, and functional groups across the study area

Infauna description	Infauna versus bioturbation relationship					
	<i>Db</i> (cm ² year ⁻¹)		<i>r</i> (year ⁻¹)		<i>BDF</i> (g _{dw} cm ² year ⁻¹)	
Total infauna						
Density (ind m ⁻²)	0.66**		–		0.46*	
Biovolume (ml m ⁻²)	0.51*		–		–	
Bv:A	–		–		–	
Taxa richness (number of taxa per core)	0.56**		–		0.44* ^P	
Functional richness (number of functional groups per core)	0.66***		–		0.63***	
	D	Bv	D	Bv	D	Bv
Mesofauna	0.60*	0.59**	–	–	–	–
Macrofauna	0.73***	0.53**	0.43*	–	0.58**	0.41*
Conveyors						
Meso-conveyors	–	–	–	0.42*	–	–
Macro-conveyors	–	–	–	–	–	–
(1) <i>Oligochaeta</i> spp.	–	–	0.44*	0.43*	–	–
Gallery-diffusors						
Meso-gallery-diffusor	0.82***	0.79***	–	–	0.55**	0.54**
Macro-gallery-diffusor	0.86***	0.7***	–	–	0.65***	0.54**
(1) <i>Amphipoda</i> sp.1	0.42*	0.42*	–	–	0.45*	0.45*
(1) <i>Discapsuedes surinamensis</i>	0.73***	0.73***	0.40*	0.40*	0.57**	0.57**
(1) <i>Halmyrapseudes spaansi</i>	0.79***	0.76***	–	–	0.50*	0.45*
Biodiffusors						
Meso-biodiffusor	0.62**	0.66***	–	–	0.43*	–
Macro-biodiffusor	–	–	–	–	–	–
(1) <i>Ostracoda</i> sp.	0.53*	0.52*	–	–	–	–
(1) <i>Nematoda</i> spp.	0.62**	0.63**	–	–	0.44*	0.44*
Regenerators						
Meso-regenerator	–	–	–	–	–	–
Macro-regenerator	–	–	–	–	–	–
(1) <i>Gobionellus oceanicus</i>	–	0.43*	–	–	–	–

(1) Denotes taxa in functional groups that are significantly correlated with bioturbation rates. Significant correlations are denoted by asterisks: * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$

conveyors (bare sediment: Pearson, $r_p = 0.67$, $P = 0.04$; pioneer mangroves: Spearman $\rho = 0.88$, $P = 0.01$), whereas this process was related to the total density of Nereids in the young mangroves (*Namalycastis* spp. and *Neanthes* sp.; Spearman, $\rho = 0.75$; $P = 0.02$). The intensities of the non-local transport and *BDF* increased together with the density and biovolume of Ostracodes (meso-biodiffusors) in the pioneer mangroves (Spearman, $\rho > 0.91$; $P < 0.01$).

Discussion

Methodological considerations

Spatial limitations

The dynamics of local mud bank migration and accretion compromises the access to coastal sites in French Guiana. Thus, additional bare sediment areas, pioneer mangroves, and young mangroves could not

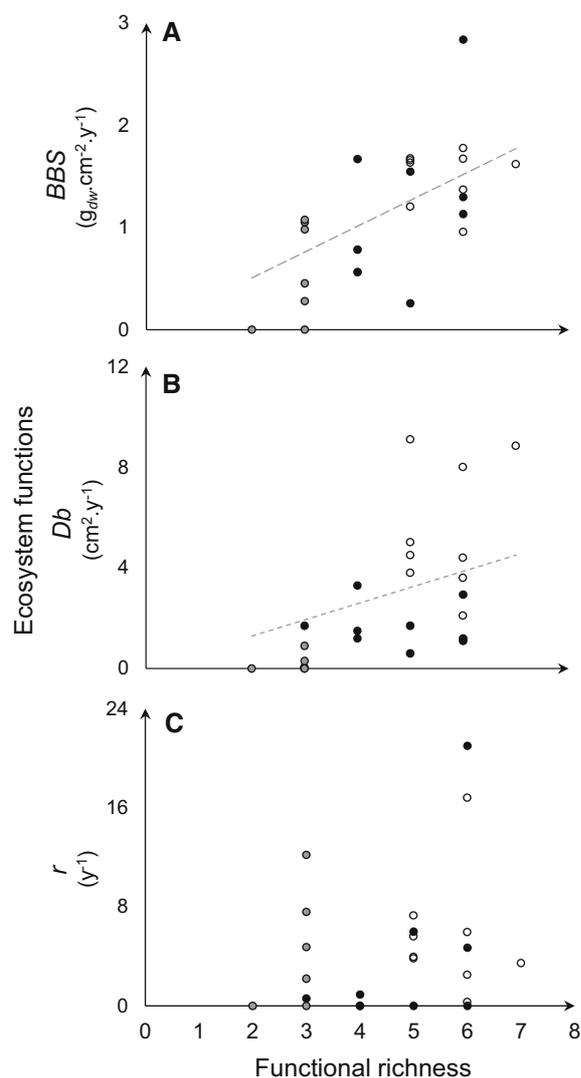


Fig. 7 Sediment reworking intensity as a function of the functional richness of the meso-macrofauna community. **A** Biological downward particle flux (*BDF*) **B** biodiffusion coefficient (*Db*), and **C** non-local transport coefficient (*r*). Spearman correlations gave ρ statistical dependency of 0.63, 0.66, and 0.22, respectively. *Dot colors* distinguish the sites: *white* bare sediment, *gray* pioneer mangroves, and *black* young mangroves. *Lines* represent the linear regression found between variables

be reached and replicated, as also found by Aschenbroich et al. (2016) in 2014 in the same Guianese study area. Sampling was thus only done during the spring tide, because a minimum water height (2.8 m) was required to access the targeted sites. This lack of site replication along the Guianese coast prevents any extrapolation of our results at the littoral scale; they

are thus cautiously inferred from the scope of the data hereafter. Nevertheless, comparable patterns may be expected in other areas along the shore under Amazonian influence (1500 km long) because it exhibits monotonous vegetation and sedimentary characteristics, being largely dominated by the tree *Avicennia germinans* (L.) Stearn and mud (Fromard et al., 1998; Anthony et al., 2010). This hypothesis needs to be confirmed by replicating sites as soon as they are accessible in further studies. Stations were, however, triplicated at each stage of mangrove development, providing relevant quantification of bioturbation by the meso- and macro-benthic biodiversity, during the spring tides in the dry season in the Sinnamary mangrove area. Our results show that sedimentary parameters varied slightly within stages of mangrove development ($SD < 16\%$ of the means, except for *Chl-a* in the young mangroves: $SD = 27\%$ of the mean; Table 1) which confirms the mangrove-age-specific environmental characteristics (Fig. 5), and thus the relevance of comparing the stages of mangrove development in this work.

Temporal limitations

Our study did not attempt to obtain the bioturbation signal during the neap tides when the young and pioneer mangroves would have emerged for 4–5 consecutive days while the bare sediment would have remained entirely immersed at each high tide. However, benthic fauna behavior may vary from neap to spring tides when the sediment reworking rates are hypothesized to be maximal. During spring tides, (1) intertidal crabs deepen their burrows to reach phreatic water levels thus increasing the sediment reworking rates (Iribarne et al., 1997), (2) organic matter inputs are high in French Guiana (Gensac et al., 2015) which is known to enhance sediment reworking by the small infauna (Nogaro et al., 2008), and (3) the sediments are wetter and softer, which would decrease burrowing costs and increase the bioturbation activities of small organisms compared to neap tide periods.

Beyond tidal cycles, bioturbation activities may vary slightly over the seasons. Seasonal variations in temperature and salinity in temperate environments influence the infauna community structure and subsequent bioturbation activities (Kristensen, 1983; Ouellette et al., 2004; Duport et al., 2007). However, such modifications are not necessarily expected in tropical

environments where the species are adapted to recurrent environmental constraints and fluctuations (Alongi, 1989). However, it has been suggested that precipitation runoff in tropical areas decreases species densities on the eastern Amazon coast (Braga et al., 2013), which could have a potential effect on the bioturbation intensity (Duport et al., 2006).

Environmental characterization

Due to sparse tree distribution in the bare sediment and pioneer mangroves, large rather than small replicated plots were studied for an accurate description of the vegetation structure following previous studies (Fromard et al., 2004; Luglia et al., 2014). Such a design prevented drawing a direct statistical relationship between the vegetation and infauna community structures. However, sedimentary habitats showed high site specificity (Fig. 5), thus responding to and representing mangrove ecosystem structuring. Indeed, the variation in sediment quality and resource may easily be ascribed to vegetation structure modifications. For instance, increasing tree density through canopy closure probably prevents sediment pore water evaporation and explains the lower sediment density in the young forest than in the bare sediment (Table 1). Thus, sediment desiccation does not increase with increasing emersion time along the elevation and mangrove development gradient. The pioneer mangroves exhibit an open canopy and a long enough tidal emersion time to favor biofilm development, as revealed by Chl-*a* concentration and total nitrogen peaks.

The direct measurement of below-ground root surface area or biomass is a labor-intensive and destructive method that could not be used in the present study. There are allometric relationships between mangrove tree diameter-at-breadth-height and below-ground biomass but they are subject to error due to sampling bias (Komiya et al., 2008): the root excavation within a metric radius around a tree includes the roots of neighboring trees, which overestimates the below-ground biomass. In the present study, only the pneumatophore density was considered and used as a proxy of the sediment structural complexity (following Morrissey et al., 2003). Although the above-ground pneumatophore density probably underestimates the below-ground root web complexity (composed of vertical cable roots

and non-emerged pneumatophores), it gives relevant information when knowing the root depth. Marchand et al. (2003) identified an oxidized layer of 30 and 50 cm in pioneer and young mangroves sediments of the Sinnamary coastal area, respectively. This layer was probably associated with the maximum depth of the mangrove main cable roots from which pneumatophores originate. Assuming that the below-ground sediment structural complexity until the maximum cable root depth is correlated with the above-ground pneumatophore density, the latter information would be a valid proxy of the structural complexity within the whole sedimentary infauna habitat considered in our study (down to a depth of 18 cm).

Bioturbation measurement

The sediment reworking measurements carried out *ex situ* did not consider the natural environmental constraints such as lateral hydrodynamics (Biles et al., 2003) or predation (Maire et al., 2010) which can inhibit infaunal activity. One may therefore expect that the *ex situ* measurements quantified the maximum biological sediment transports. Such *ex situ* measurements with a natural benthic community have been widely used in the literature (Duport et al., 2007; Cuny et al., 2015; Ferrando et al., 2015). Although the absolute values must be interpreted with caution, the relative comparisons between the stages of mangrove development remain valid. The bioturbation rates induced by natural and site-specific infaunal communities were measured herein. Communities respond to the environmental features that characterize each stage of mangrove development (Fig. 5) and are subjected to distinct immersion times due to substrate elevation along the mangrove development gradient. However, bioturbation rates were evaluated here for the same tidal period and further studies should take into account different tide conditions specific to each mangrove stage.

As pointed out by Teal et al. (2008), most of the studies concerning tropical regions lack data on the biological sediment reworking processes. Despite its limitations, the present study provides the first data about the modes and intensity of the meso- (0.25–1 mm) and macro-infauna (>1 mm)-induced sediment reworking processes in mangrove-dominated coastal areas.

Factors regulating the benthic functional diversity throughout the mangrove development

The Sinnamary infauna community was probably mesofauna dominated (Fig. 4) in response to the high coastal dynamics (mobile mud discharge, rapid mangrove development) along the coast under Amazonian influence. In fact, severe physical disturbances generally reduce the size of infauna organisms in this region (Aller & Stupakoff, 1996; Aller & Aller, 2004). Mangrove ecosystems usually exhibit low benthic taxa richness compared to adjacent ecosystems (Dittmann, 2001; Alfaro, 2006). Although direct comparisons with other studies are difficult due to the different sampling methodologies, it appears that the infaunal community in our mangrove area exhibits similar or lower taxonomic richness than the ones found in other mangrove areas.

Our results also show the site specificity of the infauna community in response to the modification of the sedimentary parameters during mangrove development. Very high densities and low organism sizes in bare sediments imply a pioneering colonization of the recently accreted sediments. The establishment of the vegetation (pioneer mangroves) coincided with a reduction in infauna densities, taxa richness, and organism sizes in relation to labile material inputs (Table 2). The pioneer mangroves exhibit an open canopy and a long enough tidal emersion time to favor biofilm development, as revealed by Chl-*a* concentration and nitrogen peaks. The dense filamentous benthic biofilm in this mangrove stage is made of cyanobacteria, which have low nutritional quality (i.e., inadequate dietary fatty acid composition; Müller-Navarra et al., 2000; Marchand et al., 2003; Debenay et al., 2007). Algal mat, which exhibits high frequency deposition in pioneer mangroves of French Guiana (Debenay et al., 2007; Gensac et al., 2015), may limit the colonization of the sensitive infauna through the limitation of larval settlement and the formation of an anoxic environment (Bolam et al., 2000; Stewart, 2003). This apparent environmental stress was also concomitant with a decrease in functional richness; the infauna community was exclusively composed of conveyor (oligochaetes) and meso-biodiffusor (Nematodes, Ostracods) functional groups, whose taxa can tolerate organic enrichment (Giere, 2006). However, these functional groups, and notably the conveying oligochaetes, remained persistent throughout

the early stages of mangrove development, probably due to their wide environmental tolerance (Giere, 2006). In addition, the gallery-diffusors and macro-biodiffusors were found in the bare sediment and young mangroves as a function of increasing sediment grain size and more refractory organic matter (C:N ratio, Table 2). Interestingly, sediment carbon contents decreased with mangrove development despite the increasing contribution of the litter and roots to the sedimentary habitat. Low C:N ratio highlighted the presence of algal-originated organic matter rather than vascular-originated organic matter in the sediments of the early mangrove development stages, in accordance with Marchand et al. (2003). These authors also found that the sedimentary record of higher plants only occurs once young mature forest appears.

Despite a comparable bioturbation functional composition in the bare sediment and young mangroves, larger-sized organisms were found in the young mangroves (Fig. 4). Increasing pneumatophore density at this stage may provide structural support for the burrowing activity of the large fauna (e.g., the regenerator *Uca* sp.; Bertness & Miller, 1984), and enhance particle trapping (Kathiresan, 2003) available for macro-suspension-feeders (e.g., the biodiffusors *Polymesoda aequilatera*, bivalva). Marchand et al. (2004) also showed that redox potential increases from the bare sediments to the mangrove forest in the Sinnamary estuary, suggesting oxygen releasing from roots and from small stems. Seedlings in high densities may also contribute to such sediment oxidizing (McKee, 1996). This probably favors the occurrence of some burrowing benthic species associated with roots. Increasing litter biomass in the young mangroves probably favors the occurrence of capittelids, chironomids, and isotomids, recognized as mostly detritivores in these ecosystems (Camilleri, 1992; Nagelkerken et al., 2008).

These functional modifications of the infauna community throughout the mangrove development (Fig. 5) explain changes in the mode and intensity of the sediment reworking during mangrove growth.

Actors in the sediment reworking modes along the mangrove growth gradient

The biodiffusion intensity was related to the density and biovolume of the gallery-diffusors and meso-biodiffusors all along the mangrove growth gradient.

The highest densities and biovolumes of the gallery-diffusers and meso-biodiffusers in the bare sediment induced the highest coefficients ($Db = 5.48 \text{ cm}^2 \cdot \text{year}^{-1}$). The absence of the gallery-diffusers, and the much lower densities of the meso-biodiffusers in the pioneer mangroves resulted in low coefficients ($Db = 0.21 \text{ cm}^2 \cdot \text{year}^{-1}$). Within the gallery-diffusers, the Tanaiids are likely to be a major driver of the biodiffusion process in the bare sediment (*Halmyrapseudes spaansi*, *Discapseudes surinamensis*; Table 4), as observed by Dupont et al. (2006) and De Backer et al. (2011) when measuring the density effects of gallery-diffusers on sediment mixing rates. In spite of their large size, gallery-diffusers in the young mangroves induced lower biodiffusion rates than in the bare sediment. The larger surface area of organisms in young mangroves may create higher friction constraints within sediments, thus increasing the energetic cost and frequency of burrowing and decreasing the local transport of sediments (Majdi et al., 2014). Such constraints may also be induced by the subsurface rhizome network in young mangroves, which may limit the biodiffusion processes (Suzuki et al., 2012; Bernard et al., 2014). Likewise, the dense filamentous algal mats spreading over the pioneer mangrove sediment surface and subsurface (Debennay et al., 2007; Gensac et al., 2015), also present at the core sediment surfaces, may inhibit directly (i.e., physically) solute diffusion in the sediment (Stewart, 2003) and/or indirectly because cyanophyceae-dominated algal mat would not be a good food resource for gallery-diffusers (inversely correlated to Chl-*a*; Table 2). Despite a strong decrease in biodiffusion rates in the pioneer mangroves, the process was detected and associated with the meso-biodiffusers. This suggests the importance of the mesofauna and its ability to dominate this process in agreement with Aller & Aller (1992) who reported the major contribution of nematodes to solute biodiffusion.

Remarkably, in the pioneer stage specifically, these results associated the Ostracod activity with non-local transport rather than biodiffusion. Generally, the intense and shallow burrowing activity of the ostracods participates in homogeneous subsurface disruption (De Lucas Pardo et al., 2013). Their low density associated with high concentrations of filamentous algae in the pioneer mangroves may reduce the local biodiffusive transport. Particles may rather settle at the burrow bottom resulting in subsurface tracer peaks.

Ostracods may also be indirectly associated with non-local transport by promoting the predatory activity of conveyors (Green, 1954). Ostracods could therefore impact sediment reworking in different ways as a function of environmental changes.

Non-local transport was related to the conveyor and gallery-diffuser groups. Interestingly, although fiddler crabs are well-known key actors in mangrove sediment processing (Gardner et al., 1987; Kristensen, 2008), the juveniles of crabs collected in this study did not promote non-local transport. Crabs' burrow maintenance activity can result in excavation of sediments from depth to the sediment surface. It may lead to the covering and subsequent burying of the surface sediment. However, this process would probably need more than 10 days of activity to be detected. In any case, juveniles of *Uca* spp. probably did not dominate sediment reworking processes as they usually inhabit burrows of others (Crane, 1975). Nevertheless, it cannot be excluded that the activity of crab juveniles was modified due to the small experimental unit size (ca. 84.9 cm^2) or the way the tide was manually simulated in the context of our study. Indeed, fiddler crab bioturbation activity is rhythmized by tidal cycles (de la Iglesia et al., 1994), which induce sediment pore water flow that precedes the tidal inundation and exudation (Xin et al., 2009). This underground water flow was, however, not mimicked by our ex situ system since only the overlying water was replaced.

Our study reveals that, despite the modification of total densities, biovolumes and the functional composition of infauna communities, the mean non-local transport of sediments was comparable between mangrove stages. The dominant functional group shifted from the meso-conveyors (pioneer mangroves) to the conveyors *plus* the gallery-diffusers (bare sediment and young mangroves). The coupled bioturbation activity of conveyors and gallery-diffusers in the latter mangrove stages did not increase the non-local transport rates. It may either suggest that (1) the transport induced by one group is balanced by the activity of the other; or (2) the bioturbation activities of one group is inhibited when both groups are present. In the young mangroves specifically, the non-local transport was related to the density of gallery-diffusers (all Nereids) and not to conveyors despite their higher density. One may hypothesize that the burrowing behavior of conveyors was modified due to spatial

interactions between functional groups (Michaud et al., 2009). This result could support the hypothesis that ecosystem processes were driven by the most efficient functional group of the community (Mermillod-Blondin et al., 2005) such as the meso- and macro-gallery-diffusers in the young mangroves. On the contrary, the conveyors were probably main actors of the non-local transport in the pioneer mangroves. Either the absence of other functional groups or the input of labile organic matter (biofilm) in the pioneer mangrove sediments may stimulate the conveyor activity, as has been shown for gallery-diffusers (Nogaro et al., 2008). The omnipresence of conveyors, whose density and biovolume slightly varied (Fig. 4) among mangrove stages, may play a non-local transport buffering role along the mangrove gradient.

Infauna community variables versus bioturbation relationships

This study shows that the intensities of biodiffusion, and subsequently of the total biological downward particle flux (*BDF*), may be predicted from the co-varying infauna primary variables (Table 4; Fig. 7). These rates were particularly linked to the functional richness ($\rho = 0.66$ and $\rho = 0.63$, Table 4), which implies that each functional group supported the functions of biodiffusion and total downward particle flux, and contributed additively to the process. Our results are in line with the theory of Cardinale et al. (2002), which states that increasing the diversity enhances the probability of positive interactions for ecosystem processes, i.e., biodiffusion and burying functions. One should recall that the number of functional traits considered in analyses determines the functional richness value and diversity–function relationships (Petchey & Gaston, 2006). However, the correlation coefficients and significances obtained in the present study (Table 4) confirm that size and sediment reworking behavior were relevant functional traits to consider and relate to the sediment reworking rates. Moreover, the community structure, the species identity, and the environmental conditions may have interacted and reduced the correlation coefficients between variables. For instance, the biodiffusion intensities expressed by the communities composed of five and six functional groups were highly variable (Fig. 7). This confirms that other factors acted along with the functional richness in determining the

sediment mixing intensity, such as the mangrove stage or the density of benthic organisms. High organism densities in the bare sediment enhanced biodiffusion rates, driving a linear and positive relationship between them ($\rho = 0.66$; Table 4). Biodiffusion also increased with the total biovolume but with lower statistical dependency ($\rho = 0.51$; Table 4). The importance of the monospecific population densities and individual biovolumes has already been shown (Duport et al., 2006; Gilbert et al., 2007). During burial, benthic animals primarily displace the particles that surround their body, in proportion to their volumetric size (Gilbert et al., 2007). This study rather suggests the relevance of the total density and biovolume to determine the biodiffusion expressed ultimately by a multi-species community. Further investigations (i.e., additional samples) are required in order to help reduce the variability of the sediment reworking rates—benthic community variables relationships.

Variations in the non-local transport rates occurred in the investigated sediments, but were not related to the primary community variables or specific to the stage of mangrove development (Tables 3, 4). However, our results slightly linked the non-local transport to the density and/or the biovolume of some particular taxa (*Oligochaetes*, *Discapseudes surinamensis*, Nereids) or functional groups (meso-conveyors; Table 4). This suggests the key importance of taxa or functional group identity for some ecosystem functions, i.e., the non-local transport therein, rather than the number of taxa/functional groups per se as previously observed (Mermillod-Blondin et al., 2005; Mokany et al., 2008). However, a similar species or functional group may have a context-specific behavior depending on environmental conditions and biological interactions, which can facilitate or inhibit some ecosystem processes (Loreau & Hector, 2001; Cardinale et al., 2002; Michaud et al., 2009). The relative idiosyncrasy between infauna variables and the non-local transport measured in this study may therefore result from the complex and highly variable biotic and abiotic interactions that characterize mangrove ecosystems (Chapman et al., 2010).

Net sediment reworking rates and functional implications

Estimating the biological downward particle flux (*BDF*) enabled the integration of the sediment reworking

process due to the infaunal activities in an overall context. *BDF* quantified the amount of particles buried from the surface, taking into account all the modes of mixing and the variations in surface sediment density. The results show that the activities of the gallery-diffusers and meso-biodiffusers ultimately determined the particle flux. The contribution of the small benthic infauna to the total biologically induced sediment mixing did not respond linearly to mangrove establishment and growth. The pioneering community, largely mesofauna-dominated, in the bare sediment highly reworked the sedimentary habitat. This study therefore suggests the importance of organisms that first colonize recently deposited sediments, and could subsequently determine the establishment of the next benthic species involved in the ecosystem development sequence. Indeed, bioturbation may be a facilitating or inhibitory process for benthic macrofauna colonization processes following sedimentary disturbances (Norkko et al., 2002; Thrush et al., 2003). Although the pioneer stage of mangrove development constrained the community structure and the biologically induced sediment reworking rates, the development into young mangroves led to increasing functional richness and total biological downward flux. Through sediment reworking activities, the infauna enhances pore water nutrient release towards the overlying water (Biles et al., 2002; Michaud et al., 2006). One may hypothesize that this activity influences oxygen and nutrient bioavailability for pneumatophores and below-ground roots, and toxin evacuation (salt, sulfides) from sediments. Further studies are required to evaluate the contribution of the small infauna sediment reworking activity to the enhancement of nutrient fluxes and mangrove primary production and faced with the mangrove crab contribution (Kristensen and Alongi, 2006; Smith et al., 2009)

Conclusion

The present study demonstrates and quantifies the importance of the small-sized infauna communities in the sedimentary functioning of highly dynamic Guianese mangroves from their establishment to their early development. Despite a low taxonomic richness and a dominance of mesofauna, biological sediment reworking is omnipresent in the targeted Sinnamary sites. The meso-conveyor functional group maintains similar rates of non-local transport at each stage of

mangrove development, despite local environmental constraints, and reduction of the community diversity, density, and biovolume. On the contrary, biodiffusion was related to the infaunal community variables (functional richness, density) along the mangrove development gradient. The high biodiffusive coefficients measured in bare sediments, newly inhabited by meso and macrofauna, induce total particle downward fluxes as high as in young mangroves.

Site replication, temporal monitoring, and older mangrove stages should be included in further studies to complete the sediment reworking description throughout mangrove development. In situ methods for sediment reworking measurement should also be considered in the future in order to include more natural environmental forcing in the description of mangrove infauna behavior and role. Specifically, mangrove small-infaunal bioturbation measurement studies are needed in order to fill the gaps in knowledge about their role in sediment reworking of mangrove coastal areas.

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