

Shifts between biotic and physical driving forces of species organization under natural disturbance regimes

Dominique Monti and Pierre Legendre

Abstract: The high ecological values (i.e., the benefits that space, water, minerals, biota, and all other factors that make up natural ecosystems provide to support native life forms) and diversities found in tropical islands emphasize the importance of incorporating disturbance into ecological models. This is of major concern in appreciating how species will survive and adapt to changes and the consequences expected in terms of biodiversity. We predicted that in lotic systems, modification to natural disturbance regimes (fluvial action) would have strong consequences on community organization, with strong disturbance regimes reducing species competitive exclusion through changes in space occupation. We tested this prediction by relating microdistribution data from a crustacean species (*Atya innocous*, Decapoda, Atyidae) in small and large rivers in Guadeloupe to two, independently obtained sets of explanatory variables describing the physical environment, as well as the crustacean and fish competitors. Our results show that in rivers with high-energy flow, the driving forces for species coexistence were mostly environmental, whereas in rivers with low-energy flow, biotic interactions were prevalent. These differences linked to natural disturbance regimes revealed that disturbance was a stochastic factor, overlying the classical community-structuring factors and affecting global species relationships.

Résumé : La haute valeur écologique (c'est-à-dire les bénéfices que l'espace, l'eau, la géologie, le vivant et tous les autres éléments procurent aux écosystèmes naturels qui maintiennent les formes de vie locales) et les hautes diversités rencontrées dans les îles tropicales, renforcent l'importance de la prise en compte des perturbations dans les modèles écologiques. Ce point est important dans l'appréciation de la manière dont les espèces survivent et s'adaptent aux changements, de même que les conséquences attendues en termes de biodiversité. Nous avons formulé l'hypothèse que dans les systèmes lotiques, les modifications des régimes naturels de perturbation (action de l'eau) auront des conséquences importantes sur l'organisation des communautés avec, dans un fort régime de perturbation, une réduction de l'exclusion compétitive liée à des changements dans l'occupation de l'espace par les espèces. Nous avons testé cette hypothèse en mettant en relation des données de distribution à petite échelle de l'espèce de crustacés *Atya innocous* (Décapode, Atyidae) dans de petites et grandes rivières de la Guadeloupe avec deux ensembles indépendants de données reliant des variables explicatives environnementales avec les abondances locales de crustacés et de poissons. Nos résultats montrent que dans les rivières à fortes variations de débit, les forces qui déterminent la coexistence entre espèces sont principalement environnementales alors que dans les rivières à faibles variations de débit les interactions entre les espèces sont davantage déterminantes. Ces différences liées au régime hydrologique révèlent que les perturbations naturelles peuvent se superposer au déterminisme classique structurant les communautés pour affecter les relations globales entre les espèces.

[Traduit par la Rédaction]

Introduction

Disturbance is often presented as any discrete unpredictable event in time that opens up space, which in turn can be colonized by individuals of the same or different species (Begon et al. 1990; Whittaker 1995). This was shown in lotic environments with changes in the development of diatom communities (Peterson 1987) and stream riparian vegetation (Pettit et al. 2001). Variation in flow regime is considered the most important source of natural disturbance

in highly turbulent tropical stream systems (Jackson et al. 2001), rather than physical processes such as bed movement (Poff 1992). In these rivers, the bed is composed of large andesitic blocks, which only move under exceptionally high discharges that occur during major storms or hurricanes. The sediment charge in the water column does not originate from bed movement but from allochthonous (terrestrial) imports in the river flow.

Regarding the climatic characteristics of these regions with marked dry and wet seasons, as our measure of hydro-

Received 5 August 2008. Accepted 26 May 2009. Published on the NRC Research Press Web site at cjfas.nrc.ca on 7 August 2009. J20707

D. Monti.¹ EA926-DYNECAR, Laboratoire de Biologie Marine, Université des Antilles et de la Guyane, Campus de Fouillole, BP 592, 97159 Pointe-à-Pitre Cedex, Guadeloupe.

P. Legendre. Département de Sciences Biologiques, Université de Montréal, C.P. 6128, Succursale Centre-ville, Montréal, QC H3C 3J7, Canada.

¹Corresponding author (e-mail: dominique.monti@univ-ag.fr).

logical disturbance, we will use variables from the set of 15 variables proposed in the literature (Poff and Ward 1989): mean monthly flow during the dry and wet seasons and maximum daily flow. These are the main hydrological variables associated with flood risk evaluation in Caribbean islands (Chaperon et al. 1985). These values correspond to changes in energy flow that provoke modifications in associated and complex gradients, including water resource, river width, suspended matter, and current speed. Disturbance will not have the restrictive meaning, also encountered in the literature, of events (either biotic or abiotic in origin) that specifically destroy biomass (Dethier 1984). According to Lugo's classification for Caribbean islands (Lugo 1988) and Odum's approach based on modifications of energy transfers with disturbances (Odum 1969), the scale retained for our study refers to non-extreme disturbances represented by type 3 and type 4 events that alter the "normal" rate of material exchange, without definitely altering the basic energy signature.

Since the 1960s, disturbances are considered to be one of the major factors determining the structure of animal or plant species assemblages. They are also seen as a significant driving force governing local diversity (Connell 1978; Perry 1994). Not only current disturbance regimes, but also ancient disturbances, seem to play a key role in community maintenance and species coexistence (Mori et al. 2007). This point is important, as a part of our study was conducted intentionally during the dry season to avoid punctual biological displacement during strong discharges. Historical events (Sousa 1979; Pickett and White 1985; Reynolds 1987) are other possible sources of actual spatial patterns. A reason invoked for this influence of perturbations on species assemblages is that they can produce a spatiotemporal mosaic of patches at different successional stages (Bengtsson et al. 2000), which increases the heterogeneity of microsite structures in perturbed areas (Nakamura et al. 1997). Disturbances are considered to strongly contribute to global properties of ecosystems such as homeostasis and resilience (Nyström et al. 2000) and to synchrony over broad spatiotemporal domains (Post and Forchhammer 2002). They are considered to be a normal and ineluctable process in a dynamic and cyclic conceptual model of ecosystems succession, in which transition phases occur between periods of strong and weak species interactions (Holling 1992).

Non-neutral models of animal and plant species diversity invoke competitive ability as a major process of ecosystem organization in classical community ecology (Connell 1978; Kolasa 2006). Species interactions will affect the population dynamics of species and, thus, biodiversity and its ability to respond to environmental or anthropogenic stresses. Based on information and network theory, in which the mass action law makes the probability of reaction proportional to the concentration of reactants (Margalef and Gutiérrez 1983), the richness and complexity of species interactions are considered to be major stabilizing components of ecosystem processes. The benefits of complexity can be compared with a spatial insurance for ecosystem functioning (Loreau et al. 2003).

Disturbances are evoked as processes strongly conditioning species competition through species–species or species–

environment relationships. They interact with colonization probabilities and with extinction patterns at the large meta-community scale for communities composed of many potentially interacting species (Leibold et al. 2004). They seem to play a key role in the maintenance of biological diversity by limiting competitive exclusion (Wanink and Witte 2000) or by generating the emergence of specific responses that increase species complementarities or functional redundancy (Loreau et al. 2001). In plants, species competitive abilities were significantly correlated with disturbance and mean positions along a stress–disturbance gradient (Wilson and Keddy 1986).

Guadeloupe was called "Calaou caera" by the ancient Arawak Amerindians, which means "island of wonderful waters". Its western portion, Basse-Terre, is dominated by a volcano, La Soufrière, the slopes of which are covered by numerous tropical streams and rivers and by tropical rainforest, largely protected through a National Park status. Because of scarce human presence and little pollution, the main differences observed between the discharges of these rivers are due to the size, slope, narrowness, and shape of the catchment areas, which create strong differences in watershed time of water concentration and in the magnitude of discharge peaks. These characteristics produce an unusual ecological situation in which the same or very similar species assemblages are found in very different hydrological conditions. Because these rivers are located on the steep sides of a volcano, their flows are turbulent, with rough water surface, waves, and bubbles (Gordon et al. 2004). The reactive time between rain events and maximum flows is very short; the export of suspended matter from the catchment areas is also very important. During the wet season, daily flows in large rivers can reach a hundred times the mean annual flow at a given site (e.g., $1220 \text{ m}^3 \cdot \text{s}^{-1}$ instead of the usual $14 \text{ m}^3 \cdot \text{s}^{-1}$ for the Grande Rivière à Goyaves during storm Marilyn on 14 September 1995; this is four times the mean annual flow of the river Seine in Paris). In Caribbean island freshwater ecosystems, where turbulent flow occurs, the aquatic fauna is almost exclusively composed of fish and macrocrustacean species (and 70% to 90% of species richness is based on macrocrustacean species alone). Insect larvae represent a very small biomass in the most downstream portions of rivers, with nanism of individuals (Coat et al. 2009).

Hydrological and associated suspended matter variation observed in large rivers, which are much more important in the tropics than in temperate regions (Bonell and Bruijnzeel 2005), represent real disturbances for fish and crustaceans with branchial filaments; very small rivers are saved from such strong events.

Our hypothesis is that disturbance regimes through fluvial action represent major structuring factors that induce adapted functionalities of organisms (fish and crustaceans) to ecosystems. Because the spatial distributions of species are a major component organizing species interactions, we will use distributions as cues in our research. Can we identify key factors determining species distributions under strong and weak flow regimes? Are these factors the same? If not, can we determine their consequences in terms of species interactions?

Materials and methods

Spatial microdistribution analyses

Sampling

The river reaches included in this study are located in the volcanic part of Guadeloupe, the Basse-Terre Island; they are homogeneous in their geomorphic features, river bed substratum (andesitic rocks), and hydromorphological facies (riffles); and they are all located in nonanthropized areas (Fig. 1). Despite the lack of regularly collected flow data for Guadeloupe rivers due to the scarcity of flow surveys in small tropical islands, six rivers belonging to two very contrasted groups of widths of their minor beds were retained. All rivers in this study belong to the “perennial runoff” (PR) category proposed by Poff (1996). The attributes of the six selected rivers and the available flow data are summarized, and the classification into two disturbance regime categories (weak, strong) derived from these data is shown (Table 1).

In each river, crustaceans and fish were collected by electrofishing during the dry season, between January and April 2005, along a single reach using a backpack electroshocker (DEKA 3000 Lord; DEKA-Gerätebau, Marsberg, Germany), beginning downstream. The dry season is separate in time from the strong punctual wet-season hydrologic events that can modify species distributions. Each sampling site was approximately 300 m². The surface was regularly sampled by contiguous quadrats of 2 m × 2 m, which were spatially referenced on a map (Supplemental Appendix S1²). Each surface was sampled three times to collect the entire species assemblages.

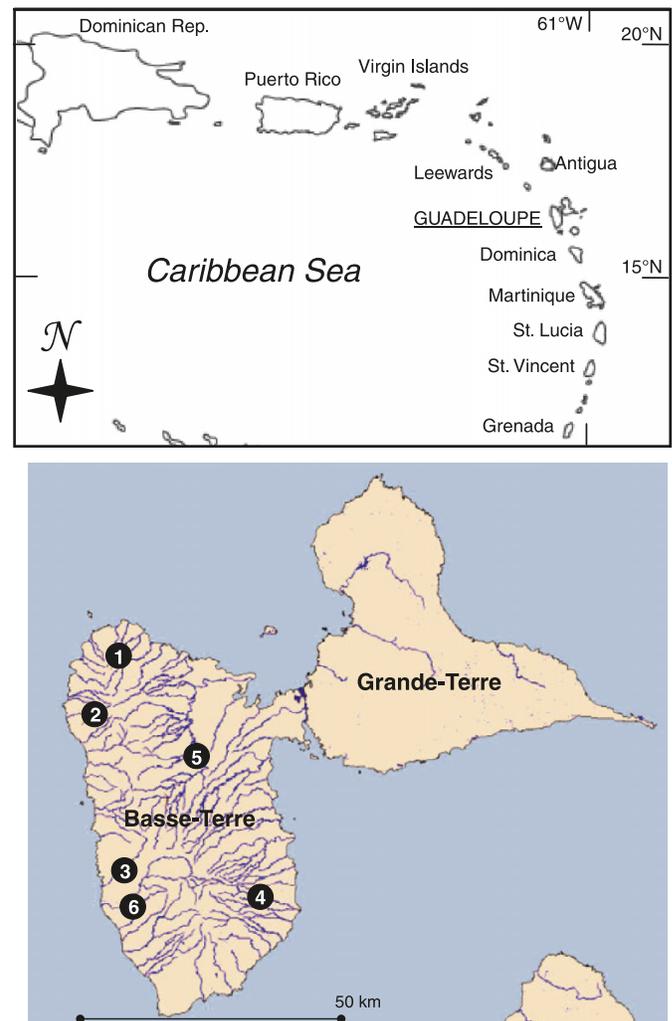
The size of quadrats was determined by the constraints of the electrofishing methods and the strong ionic content of freshwaters in Guadeloupe Island. Smaller areas would have led to bias and electrofishing contamination between patches. In each quadrat, all fish and crustaceans were identified to species and counted. At the same time, details of the microhabitat within each quadrat were recorded: mean water speed (C2 current meter; OTT GmbH, Kempten, Germany), mean water depth, size of the two main substrate classes, and a semiquantitative index of organic matter sedimentation. Four measures of current velocity and substrate size were taken for each quadrat and the mean value was retained.

Small buckets were positioned throughout each site, allowing fish and crustaceans to be released, alive, after counting.

Data analysis

The spatial microdistribution of *Atya innocous* (Herbst), Crustacea, Atyidae) was modelled by PCNM analysis (principal coordinates of neighbour matrices; Borcard and Legendre 2002; Borcard et al. 2004) and variation partitioning in the six river reaches separately. PCNM variables represent a spectral decomposition of the spatial relationships among the sampling grid cells; they describe variation at all spatial scales that can be accommodated in the sampling design.

Fig. 1. Location of the six rivers under study in the Basse-Terre portion of Guadeloupe dominated by a chain of volcanoes. Rivers: 1, Nogent; 2, Baillargent; 3, Beaugendre; 4, Capesterre; 5, Bras David; 6, Vieux Habitants.



The PCNM eigenfunctions are generated from the coordinates of the points of the sampling grid, as described in the above-mentioned papers. In the present study, we used a truncation distance that retained the horizontal, vertical, and diagonal links between neighbouring cells within each reach. A forward-selection procedure was used to identify parsimonious subsets of PCNM variables that significantly explained the spatial distributions of the species data and discard non-significant and noisy variables. Forward selection (with permutation tests, at the 5% significance level, of the increase in R^2 at each selection step) was computed using the package “packfor” (Stéphane Dray, Laboratoire de Biométrie et Biologie Évolutive, UMR CNRS 5558, Université Lyon I, France). The “PCNM” and “packfor” R-language packages are presently available at http://r-forge.r-project.org/R/?group_id=195.

²Supplementary data for this article are available on the journal Web site (<http://cjfas.nrc.ca>) or may be purchased from the Depository of Unpublished Data, Document Delivery, CISTI, National Research Council Canada, Building M-55, 1200 Montreal Road, Ottawa, ON K1A 0R6, Canada. DUD 3983. For more information on obtaining material refer to <http://cisti-icist.nrc-cnrc.gc.ca/eng/ibp/cisti/collection/unpublished-data.html>.

Table 1. Basic information about the six rivers under study.

River	Altitude (m)	Bed width (m)	No. of quadrats	Mean monthly flow (m ³ ·s ⁻¹)		Maximum daily flow (m ³ ·s ⁻¹)	Perturbation regime
				Dry season	Wet season		
1. Nogent	200	9	80	0.5 (200)	NA	26.0 (160)	Weak
2. Baillargent	230	12	83	0.2 (230)	1.8 (80)	NA	Weak
3. Beaugendre	160	10	80	0.1 (77)	0.8 (77)	8.0 (77)	Weak
4. Capesterre	170	35	80	2.6 (95)	4.4 (95)	364.0 (95)	Strong
5. Bras David	130	37	81	2.1 (130)	5.3 (130)	293.0 (130)	Strong
6. Vieux Habitants	100	44	99	2.7 (5)	4.2 (5)	410.0 (5)	Strong

Note: For flow data, altitude (in metres) at the point of the measure is in parentheses. Flow data are from the grey literature (unpublished typewritten and handwritten data) of Institut de Recherche pour le Développement (IRD, previously called Office de la Recherche Scientifique et Technique Outre-Mer, (ORSTOM), 44 bd de Dunkerque, 13572 Marseille Cedex 02, France), responsible for the hydrological surveys in Guadeloupe from 1951 to 1993, and from a synthesis of the flow data from 1951 to 1978 (Chaperon et al. 1985). NA, information not available.

Table 2. Physical characteristics of the three reaches (altitudes of 60, 130, and 230 m above sea level (a.s.l.)) sampled four times at regular intervals (1–4) and used in CCA (width of the minor bed (m), percentage of surface constituted by riffles, and mean water speed (cm·s⁻¹)).

	Reach 1 (60 m a.s.l.)				Reach 2 (130 m a.s.l.)				Reach 3 (230 m a.s.l.)			
	1	2	3	4	1	2	3	4	1	2	3	4
Width (m)	35	39	32	36	23	26	21	19	12	9	7	11
Riffles (%)	18	21	8	17	66	72	54	43	100	100	91	100
Mean speed (cm·s ⁻¹)	23	30	12	21	44	35	26	20	86	74	45	62

The spatial distributions of *A. innocuus* were then confronted to biological (other species of fish and crustaceans present in the same quadrat) and physical variables by variation partitioning through canonical redundancy analysis (RDA; Rao 1964). The technique of variation partitioning determines how much of the variation of a response variable or data table (here, *Atya*) is explained by linear models of two or more sets of explanatory variables (Borcard et al. 1992; Borcard and Legendre 1994; Legendre and Legendre 1998). The canonical analyses, variation partitioning, and tests of significance of the fractions were computed using the “vegan” library (Oksanen et al. 2009) of the R statistical language (R Development Core Team 2008). This package contains a function (“varpart”) for partitioning the variation of a response data vector or table as a function of two, three, or four tables of explanatory variables.

Species optima along disturbance gradients

Sampling

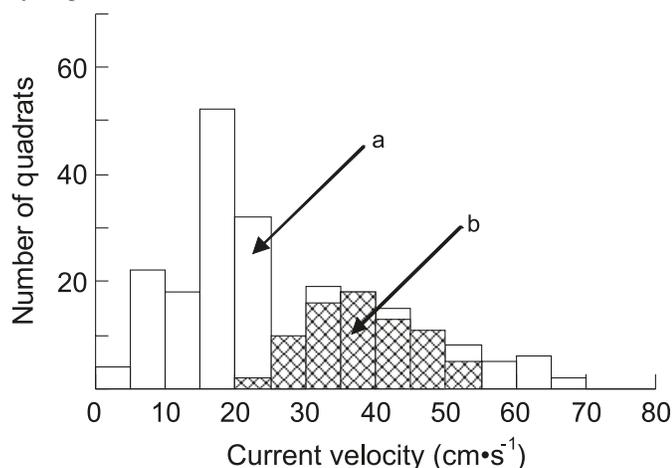
Three reaches with lengths 10 times the width of the minor riverbed were sampled four times at regular intervals between January and December 1996 along the Grande Rivière à Goyaves and its affluent, Rivière Bras David. The reaches were located at three elevations following the natural altitude variation: 230, 130, and 60 m above sea level. The species were collected by electrofishing with a replicated stratified sampling design, that is, four 3 m × 3 m surfaces in all hydromorphodynamic facies encountered (pool, riffle, cascade), to obtain a good estimation of the species–environment relationship in each facies. The total sampling effort, over the entire study period, represents 108 quadrats. In each quadrat, all species of crustacean and fish were identified and counted. Basic physical information

(mean depth, current speed, importance of the two main substrate classes, semiquantitative index of organic matter, percentage of canopy cover) was also recorded. All data collected during the sampling period were pooled for CCA analysis of each reach. A summary of the physical characteristics of the three reaches sampled is provided (width of the minor bed (m), percentage of surface constituted by riffles, mean water speed (cm·s⁻¹); Table 2). The highest reach (230 m) represents a narrow but very turbulent, high-energy river, the second (130 m) is characteristic of the inflexion point where the riverbed becomes wider, and the third (60 m) is characteristic of weak-energy flow in a very large bed (Table 2).

Data analysis

The links between the environmental variables and the observed abundances of fish and crustacean species, collected during the four campaigns, were quantified using canonical correspondence analysis (CCA; ter Braak 1986, 1987). In this method, the ordination axes are linear combinations of the environmental variables, whereas the relationships among species are projections of their chi-squared distances. The orthogonal projection of a species dot on a quantitative environmental vector or a canonical axis reflects the ranking of the species with respect to the environmental variable or axis (ter Braak 1987), under certain conditions (Legendre and Legendre 1998, section 11.2.2). This projection specifies the position of the centre (optimum) of the unimodal distribution of a species along an environmental variable or axis. For the present work, the species optima were computed along a composite CCA axis representing current velocity and substrate and indicative of the hydrodynamic gradient. Unimodal species response curves were constructed from the CCA results using the following formula:

Fig. 2. The preference curve method: (a) histogram of current velocities found in a river; (b) histogram of current velocities elected by a species.



$z = c \exp[-0.5(x - u)^2 / t^2]$, where the three ecological parameters of a species abundance distribution curve are c , the species' maximum abundance, u , its optimum (the value of x that gives maximum abundance), and t , its tolerance (a measure of ecological amplitude; Jongman et al. 1987, eq. 3.8). These values were obtained from the output of CANOCO (version 3.12; ter Braak 1988a, 1988b).

Species electivity

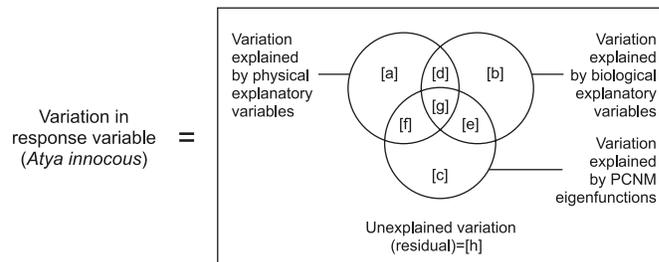
Sampling

The relationships between species and flow speeds were assessed in four rivers of the Basse-Terre Island. Two of them, Grande rivière à Goyaves and Grande Rivière de Vieux Habitants, are the two strongest and most hydrologically variable rivers of Guadeloupe. The first has flows that can vary from $1 \text{ m}^3 \cdot \text{s}^{-1}$ to more than $400 \text{ m}^3 \cdot \text{s}^{-1}$ in less than an hour; the second has a maximum daily flow estimated at $410 \text{ m}^3 \cdot \text{s}^{-1}$ during flood events (Chaperon et al. 1985). These two rivers are subjected to strong disturbance regimes. The other two (Rivière Bourceau (specific mean flow of $13.0 \text{ L} \cdot \text{s}^{-1} \cdot \text{km}^{-2}$) and Rivière Beaugendre ($14.4 \text{ L} \cdot \text{s}^{-1} \cdot \text{km}^{-2}$); Chaperon et al. 1985) were chosen for their fairly calm waters. Several reaches were chosen between 100 m and 205 m above sea level and prospected during the dry season of 2005. Stratified sampling was carried out in each river to make sure to investigate all possible situations and explore the entire gradient of speed available for colonization. Small fishing areas were explored by electrofishing, with a sampling effort of 163 to 171 sampling units, $2 \text{ m} \times 2 \text{ m}$ in size, in each river. All individuals collected were identified, and the mean values of water speed (C2 electronic current meter; OTT GmbH, Kempen, Germany) in each sampling unit were recorded at the time of sampling.

Data analysis

The preferences for intensity of hydrodynamism of four crustacean species, two Palaemonidae (*Macrobrachium crenulatum*, *Macrobrachium heterochirus*) and two Atyidae (*Micratya poeyi* and *Xiphocaris elongata*), were obtained by the classical approach used in microhabitat definition or for-

Fig. 3. Venn diagram representation of the partition of the variation of a response variable (rectangle) among three explanatory data tables: physical and biological influences and spatial structure (PCNM functions). The fractions are identified by the bracketed letters [a] to [h]; these identifiers are used in the output of the “vegan” function “varpart”. The fractions of special interest in this paper are [f] and [e].



aging behaviour studies, that is, a comparison between resource (speeds “proposed” by the river) and the class of the resource “occupied” by each species (Fig. 2). The active choice of each species was quantified by an electivity index. If positive, the index reveals a species preference; negative values indicate avoidance. When plotted in a graph, this index allows a quick visual reading of the preferential habitats of the species. The electivity index (E^*) of Vanderploeg and Scavia (1979) was used. This index was computed as $E^* = [W_i - (1/n)] / [W_i + (1/n)]$, where n represents the number of resource categories, $W_i = (r_i/p_i) / \sum(r_i/p_i)$, r is the proportion of resources utilized, and p is the proportion of resources available (Vanderploeg and Scavia 1979). This index produces, by construction, values between -1 and $+1$.

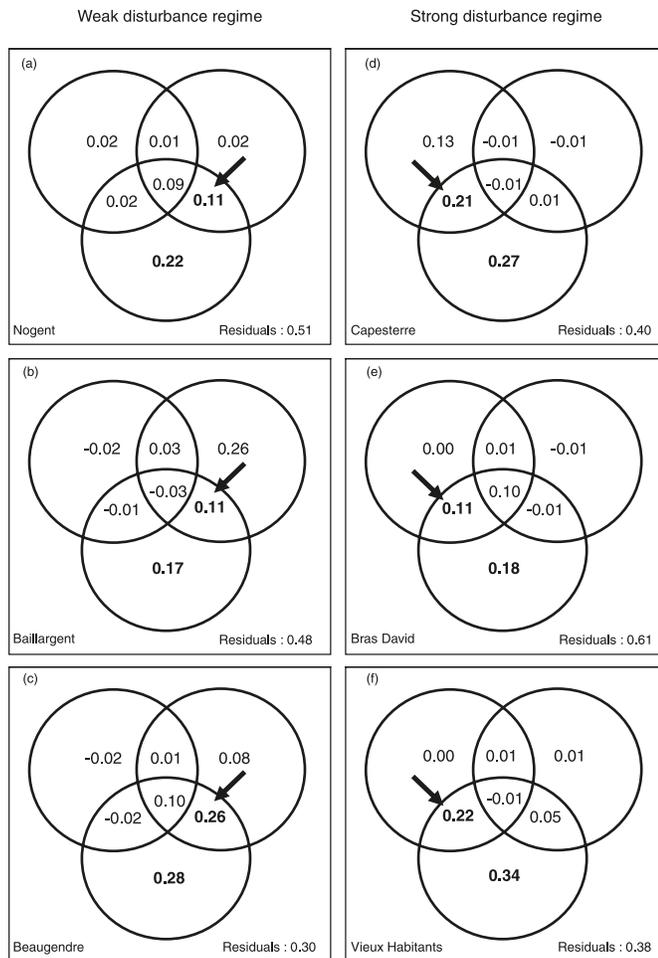
Results

Spatial structure of *A. innocuus* habitat

The geographic microdistribution of *A. innocuus* was investigated by PCNM analysis. After forward selection, all significant PCNM variables were pooled in a single spatial model and confronted, by variation partitioning, with the physical and biological explanatory data tables. The theoretical variation partitioning model is illustrated (Fig. 3). $[c + e + f + g]$ represents the variation of *A. innocuus* across quadrats that is explained by the PCNM base functions and is, thus, spatially structured. Of special interest in the present study are [f], the spatial variation of *A. innocuus* explained by physical variables, and [e], that explained by biological variables. The results in the three river reaches with weak perturbation regimes (1, 2, and 3; see Table 1) and the three with strong perturbation regime (4, 5, and 6; see Table 1) are presented (Fig. 4). The highest fraction of spatial variation and its relation to physical or biological variables is identified by an arrow in each diagram. The fractions were computed from adjusted coefficients of determination (R^2_a), as recommended by Peres-Neto et al. (2006).

The PCNM functions explained 32% to 66% of the spatial variation of *A. innocuus* in the weak perturbation regime and 40% to 62% in the strong perturbation regime (adjusted R^2). These are very high contributions to the explanation of the spatial structures. Fractions [e] and [f] are of special interest in the present study: fraction [e] estimates the portion of *Atya* variation that is spatially structured and significantly

Fig. 4. Dominant effects, physical or biological (arrows), explaining the spatial distributions of *Atya innocous* in low-energy (i.e., weak disturbance regime; left) and high-energy (i.e., strong disturbance regime; right) river reaches. The values of the fractions of variation are adjusted R^2 coefficients.



described by the PCNM eigenfunctions and also significantly explained by the biological explanatory variables. A strong fraction [e] thus indicates biological control of the spatial microdistribution of *Atya*. Fraction [f] estimates the portion of *Atya* variation that is spatially structured and significantly described by the PCNM eigenfunctions and also significantly explained by the physical explanatory variables. A strong fraction [f] thus indicates physical control of the spatial microdistribution of *Atya*. When looking at the major explanatory variables, between [e] and [f], for each disturbance regime, our results show a clear predominance of biological covariation (fraction [e]) for the weak disturbance reaches (Fig. 4, left-hand column), with values of 11%–26%, and a predominance of physical covariation (fraction [f]) for the strong disturbance reaches, with values of 11%–22% (right-hand column). Correlations between *A. innocous* and the other species present in each river are presented (Table 3). The positive and significant values ($\alpha = 0.05$) are indicated by asterisks; they indicate species that are significantly associated with *Atya* in the 2 m \times 2 m quadrats. Examination of the values shows more cohabitation in weak disturbance regimes. *Macrobrachium crenulatum*, *Macrobrachium faustinum*, and *Sicydium punctatum*,

three species that cohabit with *A. innocous* at least part of the time in weak disturbance rivers, no longer do so in strong disturbance regimes; their correlations with *A. innocous* are not significantly different from zero or negative.

Disjunction of species optima

The species response curves along a composite CCA axis representing current velocity and substrate are presented (Fig. 5), which summarizes the hydrodynamic gradient. We observed that CCA axis 1 was strongly correlated with water velocity and substrate diameter (respectively, 0.606 and 0.642 at 60 m elevation, 0.694 and 0.782 at mid-elevation, and 0.894 and 0.793 at high elevation). The species–environment correlations for the composite environmental axis (combined velocity and substrate) were 0.831 for the upstream reach (230 m), 0.819 for the mid-elevation reach, and 0.854 for the downstream reach. The height of the mode, which represents the value of parameter *c* in the equation (see Materials and methods), is the theoretical abundance at which a species has its optimum along the gradient. Two crustacean species, *M. faustinum* and *M. poeyi*, have the highest values and largest tolerances (standard deviations of the curves); they strongly dominate the species assemblages in all cases.

In a strong-perturbation regime (Fig. 5a), we observe two cohesive hydrodynamism-specific guilds: a guild of species living in low-energy flow, which includes three crustacean species (*M. faustinum*, *M. crenulatum*, and *X. elongata*), and a guild of species living in high-energy flow, which contains five crustaceans (*M. poeyi*, *M. heterochirus*, *Macrobrachium carcinus*, *Potimirim potimirim*, and *Atya scabra*) and one Gobiidae fish (*S. punctatum*; adapted to high current velocities by the presence of a sucker). The species to the right, and especially *M. heterochirus* and *M. carcinus*, have little overlap with the three species to the left.

In a weak disturbance regime (Fig. 5c), the species optima are closer. Four of the most patrimonial Caribbean freshwater species, that is, the species with high requirements for water quality, with distributions that are all in regression, are lacking: *M. carcinus*, *M. heterochirus*, *A. innocous*, and *A. scabra*. There are three “new” fish species: the tilapia *Oreochromis mossambicus* (Cichlidae), considered a biological pest because it is naturalized and invasive in the Caribbean region, and the mountain mullet, *Agonostomus monticola* (Mugilidae), which is widely distributed. The third one is the superpredator *Gobiomorus dormitor* (Eleotridae), which feeds heavily on shrimps, cichlids, and other fish (Winemiller and Ponwith 1998). Under these conditions of strong niche overlap, *M. faustinum* still has the highest abundance value. This species dominates systematically all species with optimum included under its preferendum curve, that is, all species except *S. punctatum* and *M. poeyi*. The curves of all species but *M. faustinum* are depressed, indicating general losses in abundance. There is a high degree of niche overlap among the species.

Mid-elevation (Fig. 5b) presents an intermediate situation with the persistence of patrimonial species in very small abundances and an increased overlap with the two strongest competitors, *M. faustinum* and *M. poeyi*. Comparison of the three situations shows that in a strong disturbance regime, the overlap in optima between nondominant species and

Table 3. Spatial association of *Atya innocous* with crustacean (*Macrobrachium*, *Micratya*, *Xiphocaris*) and fish (*Sicydium*) species in quadrats: correlations within each river (columns).

Species	Weak disturbance regime rivers			Strong disturbance regime rivers		
	Nogent	Baillargent	Beaugendre	Capesterre	Bras David	Vieux Habitants
<i>Macrobrachium crenulatum</i>	0.110	0.231*	0.179	-0.106	0.011	-0.106
<i>Macrobrachium faustinum</i>	0.370***	-0.029	-0.027	-0.165	0.024	-0.142
<i>Macrobrachium heterochirus</i>	0.276*	0.370***	0.505***	0.262*	0.137	0.102
<i>Micratya poeyi</i>	0.296**	0.210*	0.721***	0.235*	0.273*	-0.023
<i>Sicydium punctatum</i>	0.382***	-0.036	-0.076	0.108	0.077	0.005
<i>Xiphocaris elongata</i>	0.022	-0.101	—	-0.146	0.032	-0.102

Note: *, $0.01 < p \leq 0.05$; **, $0.001 < p \leq 0.01$; ***, $p \leq 0.001$. Otherwise, $p > 0.05$.

Fig. 5. Niche separation among the tropical freshwater species under strong disturbance regime. Altitude: (a) 230 m, (b) 130 m, and (c) 60 m.

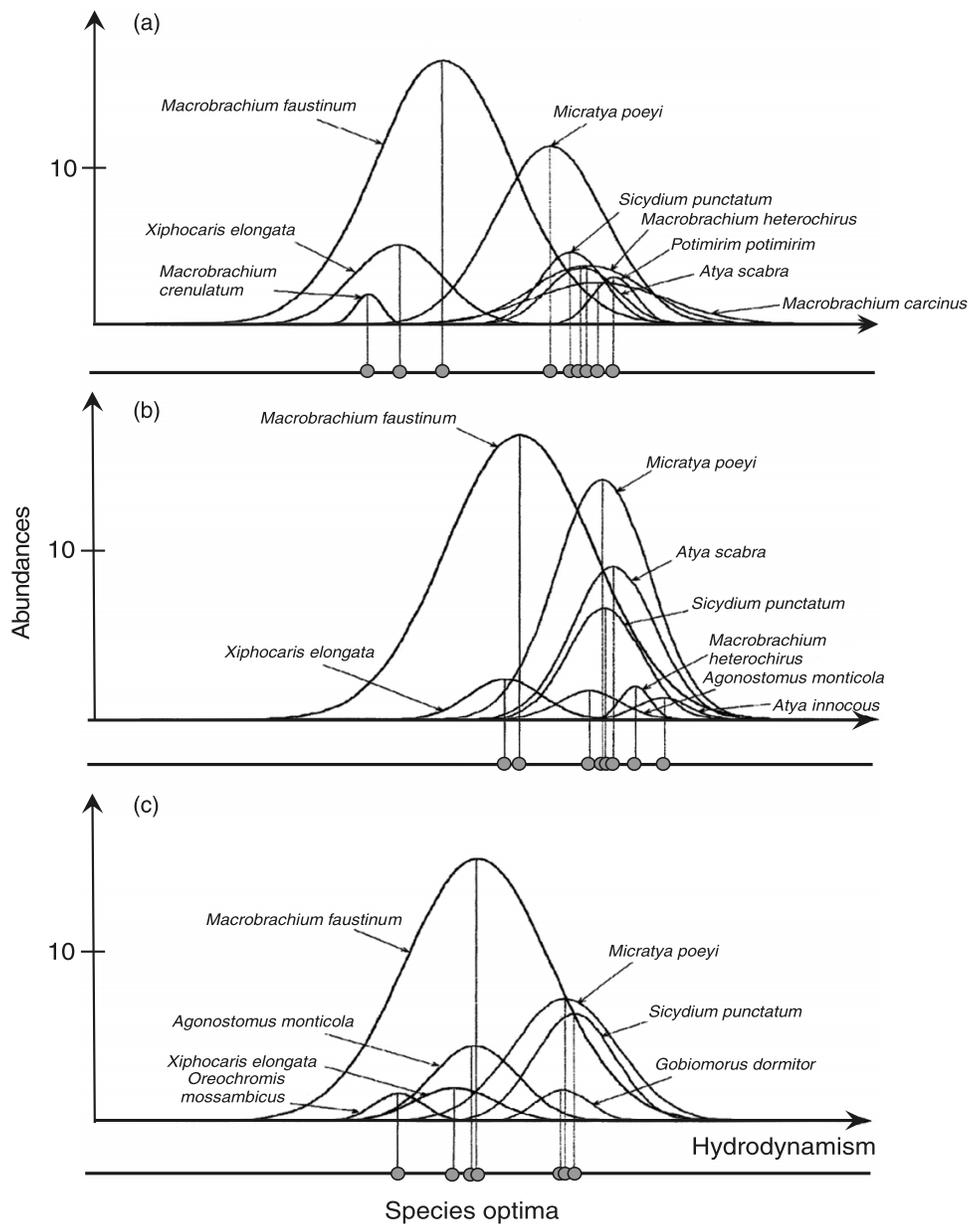
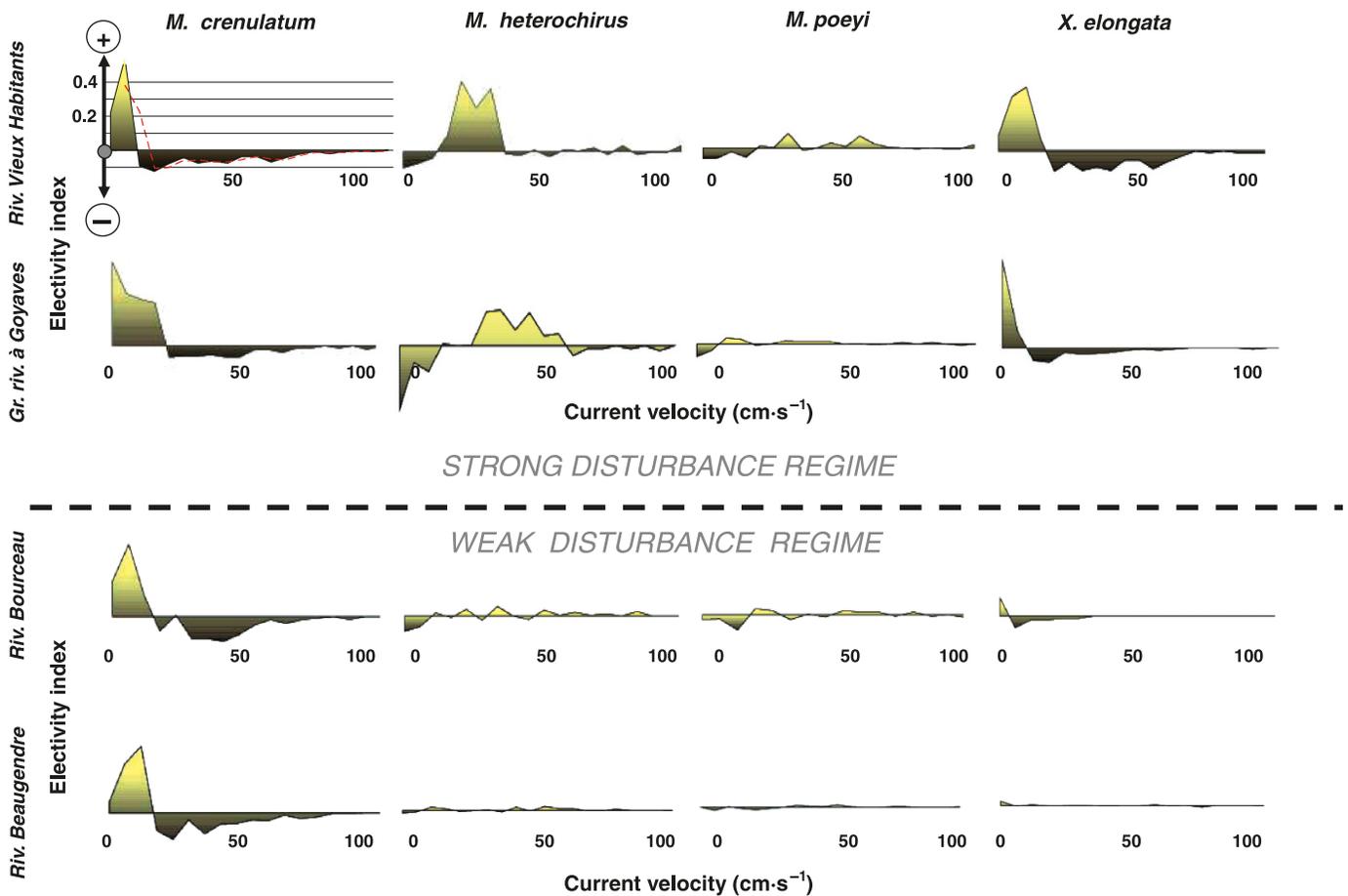


Fig. 6. Comparison of the preference curves for four species in four rivers, two with strong and two with weak disturbance regimes.



high-abundance competitors is smaller than in a weak disturbance regime.

Species electivity for current velocities

Water velocity electivity values are presented for four crustacean species in weak and strong disturbance regimes (Fig. 6). Not all species are elective. *Macrobrachium crenulatum* shows strong electivity for weak currents, with values ranging from 5 to 15 cm·s⁻¹. Its preferendum is persistent through the disturbance regimes. *Macrobrachium heterochirus* shows strong electivity for higher current velocities ranging from 20 to 55 cm·s⁻¹ in strong disturbance regimes. In weak disturbance rivers, this species has weakened electivity and broader habitat. This is also the case for *X. elongata*, which has its optimum in current velocities ranging from 5 to 15 cm·s⁻¹. *Micratya poeyi* has very small velocity requirements, whatever the disturbance regime.

Discussion

Multiscale spatial processes as a key for understanding the mechanisms controlling biodiversity in relation to natural disturbance regimes

The link between the structure of ecological systems under disturbance and the generating spatial processes has long been recognized. Important population and community processes operate at various spatial scales, and all these

processes are crucial for understanding and predicting diversity, in particular in tropical streams (Boyero and Bailey 2001). A critical question is: how can we extrapolate from ecological processes and patterns identified at small spatial scales to larger scales, and vice versa (Thrush et al. 1997). The PCNM approach used in our study describes all spatial scales, from broad to fine, that can be accommodated in the sampling design. This represented a great advantage in our study in that we did not have to decide of an a priori scale at which we would be looking for processes. We let the data speak: the distribution of *A. innocous* abundance values in the reaches was used to select the significant PCNM variables. After selection, these variables modelled the multiscale spatial structure of *Atya* abundances. It turned out that, for *Atya*, an important fraction of the variation in abundance among quadrats was spatially structured in all rivers surveyed. Such gain in spatial information allowed us to further investigate, by variation partitioning, the effects of physical and biotic processes on community organization under the two types of disturbance regimes.

Tropical rivers are resource-limited; natural disturbances enhance ecological connectivity between land and water

High-velocity and highly turbulent flows are characteristics of tropical volcanic island rivers in the major portions of their courses. This is the case in Basse-Terre Island,

where the main portions of rivers are running through high slope catchments. In these conditions, trophic resources are limited for the crustaceans and fish living therein; phytoplankton or zooplankton consumers are absent. In the lower portions of these rivers, the trophic relationships have been finely studied with stable isotopes analyses (Coat et al. 2009). The fish and crustaceans found in Guadeloupe rivers consume two types of food: (i) allochthonous, with leaves, fruits, and the drift of organic particulate matter, and (ii) autochthonous, with epilithic biofilm (heavily consumed by most of the species) and juvenile crustaceans. The work of Coat et al. (2009) also shows very strong plasticity in species food consumption throughout the hydrological seasons. In these tropical island rivers, most species are opportunistic and have access to very limited resources at any one time. This is so true that the larvae of almost all crustaceans encountered in these tropical island rivers, such as members of the genera *Macrobrachium* and *Atya*, drift with the flow during the rainy season and reach the river mouths to find planktonic resources, begin to eat food appropriate to their size, and grow. Amphidromous cycles with exported larvae are the general model for freshwater Caribbean crustaceans. Consumable organic matter for crustaceans in these aquatic systems is limited, with a preponderance of epilithic biofilm and litter or terrestrial exports. Natural disturbances induced by intense rainfall or flooding could enhance the ecological connections between terrestrial and aquatic ecosystems (Ward 1998) and, as mentioned in literature, should enhance the development of resource generalists (Poff and Allan 1995). On the other hand, anthropogenic impacts such as flow regulation works isolate river channels from riparian systems and reduce the diversity of trophic resources.

In resource-limited situations, compensatory dynamics is a mechanism defined as the tendency of competitive species to exhibit negative covariances in population dynamics, so that variables that reflect resource use are more stable than would be expected from random shifts in species composition (Ernest and Brown 2001). In a strong natural disturbance regime, our results showed a disjunction in optima of three crustacean species: *M. faustinum*, *X. elongata*, and *M. crenulatum*. The first two species are known to have their trophic behaviour more dependent on litter or terrestrial exports (Crowl et al. 2006; Wright and Covich 2005). By opening space for colonization, disturbances may alleviate co-occurrence for proximate values of the hydrodynamism gradient. Fluctuations can promote coexistence when there is extrinsic variability and species differ in which points along the fluctuations they find favourable (Chesson 2000).

Species segregation is ordinarily the result of microhabitat partitioning (biotic effects) or choice of distinct microclimates (abiotic effects). Most studies based on field observations suggest that niche segregation rather than competitive exclusion is the predominant outcome resulting from competitive interactions (Jackson et al. 2001). Habitat segregation appears to be the most prevalent resource-partitioning mechanism identified for lake and stream fish (Grossman et al. 1998). In our study, the spatial distributions of *A. innocous* reflected a behavioural adaptation of this crustacean to the two types of environment. The space-occupation strategy followed by *A. innocous* may be a response to either adaptation to the physical conditions or biotic interactions, depend-

ing on the perturbation regime. Note that the data were collected during the dry season, separated in time from the flooding episodes, which indicates that these determinisms are persistent through time. Because of strong correlations with spatially referenced abiotic variables and poor correlations with spatially referenced biotic information, the limitation of niche overlap linked to strong disturbance regimes can be suspected here to be the result of an active choice leading to a maximization of resource intake for the entire community. In that case, the paradigm of optimality, which assumes that organisms can discern among habitats those that provide greater opportunities and make appropriate “decisions” (Chase and Leibold 2003), is supported by our data. These shifts of microhabitat for coexisting species are not equivalent to those that could increase biotic costs when species move into habitat types for which they are poorly adapted, or which create new biotic interactions (Martin 2001).

Decoupled species disturbance sensitivity

In assessments of the effects of disturbance on species assemblages, we generally consider that all species equilibria are affected, without considering the sensitivities of individual species. In their study of vegetation disturbance, Bascompte and Rodríguez (2000) concluded that the modified habitat quality could only accommodate a restricted group of species and that some species were only able to use the newly available resources. Our results show that some species are more reactive to disturbance than others. In the scale of disturbance regimes studied here, if one considers the hydrodynamism gradient as an axis of the realized niches of river species, we can recognize three modes of sensitivity. The first is independence of the disturbance regime, with strong electivity for specific conditions, like *M. crenulatum*. Whatever the disturbance regime, this species retains its electivity for very mild currents and does not broaden its habitat to include stronger currents. The second mode is independence of the disturbance regime with low (or no) electivity, like *M. poeyi*. This is the smallest freshwater crustacean in the West Indies (mature at 15 mm in length); it colonizes all hydrodynamic facies, whatever the disturbance regime. The third mode, of special interest here, concerns species that are highly sensitive to the disturbance regime and strongly modify their habitat electivity accordingly; *M. heterochirus* and *X. elongata* represents that mode. Species in that group need to have high behavioural plasticity. Assemblages containing species pertaining to these different modes make it possible, during a disturbance, to have a species fleeing a type of habitat (“fugitive species”) while others are colonizing it (Graniero 2007).

Practical implications in terms of biodiversity management

In Guadeloupe, 80% of the freshwater consumed by humans originates from surface water abstraction. To preserve a minimal flow downstream is now a legal obligation. The notion of minimal flow, that is, the minimal level of aquatic resources required for maintaining aquatic life, appeared only lately in France. Based on hydrological data, the “minimum minimorum” is formerly defined by law as a fraction of the mean interannual flow at the point of im-

poundment. Legal guidelines for an optimization of minimal flow values taking into account the real needs of species are lacking, however. A minimum acceptable flow evaluated on a biological basis, instead of on hydrological data, is a method largely employed in Europe (Lamouroux et al. 1999). The goal of this state-of-the-art method, which is based on biological requirements, is to send sufficient water resources downstream so as to preserve minimal potential habitats for the species. This work involves computing habitat suitability curves associating various life stages or activities of the species of interest with three main variables: velocity, depth, and substrate type. In our study, we have seen that the relationships between the species and the physical characteristics of their habitat are strongly dependent on the perturbation regimes. In the small rivers that we studied, the species distributions were more influenced by biotic interactions than by physical processes. These small rivers, called “ravines” by Guadeloupians, are appreciated for their ability to maintain high aquatic biodiversity in a small amount of space. This was not the case in large and highly disturbed rivers where the spatial structuring was more strongly linked to the physical variables. These observations confirm the urgent need to determine species optima with due consideration for perturbation regimes. This is a prerequisite for the efficient protection of aquatic diversity in tropical rivers.

Acknowledgements

The authors thank Erwann Gouezec for assistance during fieldwork and Jean-François Nedelec (Direction Régionale de l'Environnement Guadeloupe) for the map of Guadeloupe and perennial rivers shown in Fig. 1. This research was funded by grants from the Direction Régionale de l'Environnement Guadeloupe and the Parc National de la Guadeloupe to D. Monti and by Natural Sciences and Engineering Research Council of Canada (NSERC) grant 7738 to P. Legendre. The experiments comply with the current laws of the country in which they were performed.

References

- Bascompte, J., and Rodríguez, M.A. 2000. Self-disturbance as a source of spatiotemporal heterogeneity: the case of the tallgrass prairie. *J. Theor. Biol.* **204**(2): 153–164. doi:10.1006/jtbi.2000.2002. PMID:10887898.
- Begon, M., Harper, J.L., and Townsend, J.R. 1990. *Ecology: individuals, populations and communities*. 2nd ed. Blackwell, Boston, Mass.
- Bengtsson, J., Nilsson, S.G., Franc, A., and Menozzi, P. 2000. Biodiversity, disturbances, ecosystem function and management of European forests. *For. Ecol. Manage.* **132**(1): 39–50. doi:10.1016/S0378-1127(00)00378-9.
- Bonell, M., and Bruijnzeel, L.A. (Editors). 2005. *Forests, water and people in the humid tropics: past, present and future*. Hydrological research for integrated land and water management. Cambridge University Press, Cambridge, UK.
- Borcard, D., and Legendre, P. 1994. Environmental control and spatial structure in ecological communities: an example using oribatid mites (Acari, Oribatei). *Environ. Ecol. Stat.* **1**(1): 37–61. doi:10.1007/BF00714196.
- Borcard, D., and Legendre, P. 2002. All-scale spatial analysis of ecological data by means of principal coordinates of neighbor matrices. *Ecol. Model.* **153**(1–2): 51–68. doi:10.1016/S0304-3800(01)00501-4.
- Borcard, D., Legendre, P., and Drapeau, P. 1992. Partialling out the spatial component of ecological variation. *Ecology*, **73**(3): 1045–1055. doi:10.2307/1940179.
- Borcard, D., Legendre, P., Avois-Jacquet, C., and Tuomisto, H. 2004. Dissecting the spatial structure of ecological data at multiple scales. *Ecology*, **85**(7): 1826–1832. doi:10.1890/03-3111.
- Boyero, L., and Bailey, R.C. 2001. Organization of macroinvertebrate communities at a hierarchy of spatial scales in a tropical stream. *Hydrobiologia*, **464**(1/3): 219–225. doi:10.1023/A:1013922307096.
- Chaperon, P., L'Hote, Y., and Vuillaume, G. 1985. *Les ressources en eau de surface de la Guadeloupe*. Monographies hydrologiques ORSTOM. Vol. 7. ORSTOM, Paris, France.
- Chase, J.M., and Leibold, M.A. 2003. *Ecological niches: linking classical and contemporary approaches*. University of Chicago Press, Chicago, Illinois.
- Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.* **31**(1): 343–366. doi:10.1146/annurev.ecolsys.31.1.343.
- Coat, S., Monti, D., Bouchon, C., and Lepoint, G. 2009. Trophic relationships in a tropical stream food web assessed by stable isotope analysis. *Freshw. Biol.* **54**(5): 1028–1041. doi:10.1111/j.1365-2427.2008.02149.x.
- Connell, J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science (Washington, D.C.)*, **199**(4335): 1302–1310. doi:10.1126/science.199.4335.1302. PMID:17840770.
- Crowl, T.A., Welsh, V., Heartsill-Scalley, T., and Covich, A.P. 2006. Effects of different types of conditioning on rates of leaf-litter shredding by *Xiphocaris elongata*, a Neotropical freshwater shrimp. *J. N. Am. Benthol. Soc.* **25**(1): 198–208. doi:10.1899/0887-3593(2006)25[198:EODTOC]2.0.CO;2.
- Dethier, M.N. 1984. Disturbance and recovery in intertidal pools: maintenance of mosaic patterns. *Ecol. Monogr.* **54**(1): 99–118. doi:10.2307/1942457.
- Ernest, S.K.M., and Brown, J.H. 2001. Homeostasis and compensation: the role of species and resources in ecosystem stability. *Ecology*, **82**(8): 2118–2132. doi:10.2307/2680220.
- Gordon, N.D., McMahon, T.A., Finlayson, B.L., Gippel, C.J., and Nathan, R.J. 2004. *Stream hydrology: an introduction for ecologists*. 2nd ed. John Wiley & Sons, New York.
- Graniero, P.A. 2007. The influence of landscape heterogeneity and local habitat effects on the response to competitive pressures in metapopulations. *Ecol. Model.* **203**(3–4): 349–362. doi:10.1016/j.ecolmodel.2006.12.002.
- Grossman, G.D., Ratjczak, R.E., Jr., Crawford, M., and Freeman, M.C. 1998. Assemblage organization in stream fishes: effects of environmental variation and interspecific interactions. *Ecol. Monogr.* **68**: 396–420.
- Holling, C.S. 1992. Cross-scale morphology, geometry, and dynamics of ecosystems. *Ecol. Monogr.* **62**(4): 447–502. doi:10.2307/2937313.
- Jackson, D.A., Peres-Neto, P.R., and Olden, J.D. 2001. What controls who is where in freshwater fish communities — the roles of biotic, abiotic, and spatial factors. *Can. J. Fish. Aquat. Sci.* **58**(1): 157–170. doi:10.1139/cjfas-58-1-157.
- Jongman, R.H.G., ter Braak, C.J.F., and van Tongeren, O.F.R. (Editors). 1987. *Data analysis in community and landscape ecology*. Pudoc, Wageningen, the Netherlands. Re-issued in 1995 by Cambridge University Press, Cambridge, UK.
- Kolasa, J. 2006. A community ecology perspective on variability in complex systems: the effects of hierarchy and integration. *Ecol. Complex.* **3**(1): 71–79. doi:10.1016/j.ecocom.2005.08.001.

- Lamouroux, N., Olivier, J.M., Persat, H., Pouilly, M., Souchon, Y., and Statzner, B. 1999. Predicting community characteristics from habitat conditions: fluvial fish and hydraulics. *Freshw. Biol.* **42**(2): 275–299. doi:10.1046/j.1365-2427.1999.444498.x.
- Legendre, P., and Legendre, L. 1998. Numerical ecology. 2nd English ed. Elsevier Science BV, Amsterdam, the Netherlands.
- Leibold, M.A., Holyoak, M., Mouquet, N., Amarasekare, P., Chase, J.M., Hoopes, M.F., Holt, R.D., Shurin, J.B., Law, R., Tilman, D., Loreau, M., and Gonzalez, A. 2004. The metacommunity concept: a framework for multi-scale community ecology. *Ecol. Lett.* **7**(7): 601–613. doi:10.1111/j.1461-0248.2004.00608.x.
- Loreau, M., Naeem, S., Inchausti, P., Bengtsson, J., Grime, J.P., Hector, A., Hooper, D.U., Huston, M.A., Raffaelli, D., Schmid, B., Tilman, D., and Wardle, D.A. 2001. Biodiversity and ecosystem functioning: current knowledge and future challenges. *Science (Washington, D.C.)*, **294**(5543): 804–808. doi:10.1126/science.1064088. PMID:11679658.
- Loreau, M., Mouquet, N., and Gonzalez, A. 2003. Biodiversity as spatial insurance in heterogeneous landscapes. *Proc. Natl. Acad. Sci. U.S.A.* **100**(22): 12765–12770. doi:10.1073/pnas.2235465100. PMID:14569008.
- Lugo, A.E. 1988. The wetlands of Caribbean islands. *Acta Cientifica*, **2**: 24–31.
- Margalef, R., and Gutiérrez, E. 1983. How to introduce connectance in the frame of an expression for diversity. *Am. Nat.* **121**(5): 601–607. doi:10.1086/284089.
- Martin, T.E. 2001. Abiotic vs. biotic influences on habitat selection of coexisting species: climate change impacts? *Ecology*, **82**: 175–178.
- Mori, A.S., Mizumachi, E., and Komiyama, A. 2007. Roles of disturbance and demographic non-equilibrium in species coexistence, inferred from 25-year dynamics of a late-successional old-growth subalpine forest. *For. Ecol. Manage.* **241**(1–3): 74–83. doi:10.1016/j.foreco.2006.12.031.
- Nakamura, F., Yajima, T., and Kikuchi, S. 1997. Structure and composition of riparian forests with special reference to geomorphic site conditions along the Tokachi River, northern Japan. *Plant Ecol.* **133**(2): 209–219. doi:10.1023/A:1009787614455.
- Nyström, M., Folke, C., and Moberg, F. 2000. Coral reef disturbance and resilience in a human-dominated environment. *Trends Ecol. Evol.* **15**(10): 413–417. doi:10.1016/S0169-5347(00)01948-0. PMID:10998519.
- Odum, E.P. 1969. The strategy of ecosystem development. *Science (Washington, D.C.)*, **164**(3877): 262–270. doi:10.1126/science.164.3877.262.
- Oksanen, J., Kindt, R., Legendre, P., O'Hara, R.B., Simpson, G.L., Solymos, P., Stevens, M.H.H., and Wagner, H. 2009. Vegan: community ecology package. R package version 1.15-2. Available at <http://cran.r-project.org/>.
- Peres-Neto, P.R., Legendre, P., Dray, S., and Borcard, D. 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. *Ecology*, **87**(10): 2614–2625. doi:10.1890/0012-9658(2006)87[2614:VPOSDM]2.0.CO;2. PMID:17089669.
- Perry, D.A. 1994. Forest ecosystems. John Hopkins University Press, Baltimore, Md.
- Peterson, C.G. 1987. Influences of flow regime on development and desiccation response of lotic diatom communities. *Ecology*, **68**(4): 946–954. doi:10.2307/1938366.
- Pettit, N.E., Froend, R.H., and Davies, P.M. 2001. Identifying the natural flow regime and the relationship with riparian vegetation for two contrasting Western Australian rivers. *Regul. Rivers Res. Manage.* **17**(3): 201–215. doi:10.1002/rrr.624.
- Pickett, S.T.A., and White, P.S. (Editors). 1985. The ecology of natural disturbance and patch dynamics. Academic Press, New York.
- Poff, N.L. 1992. Why disturbances can be predictable: a perspective on the definition of disturbance in streams. *J. N. Am. Benthol. Soc.* **11**(1): 86–92. doi:10.2307/1467885.
- Poff, N.L. 1996. A hydrogeography of unregulated streams in the United States and an examination of scale-dependence in some hydrological descriptors. *Freshwater Biol.* **36**: 71–91.
- Poff, N.L., and Allan, J.D. 1995. Functional organization of stream fish assemblages in relation to hydrological variability. *Ecology*, **76**(2): 606–627. doi:10.2307/1941217.
- Poff, N.L., and Ward, J.V. 1989. Implications of streamflow variability and predictability for lotic community structure: a regional analysis of streamflow patterns. *Can. J. Fish. Aquat. Sci.* **46**(10): 1805–1818. doi:10.1139/f89-228.
- Post, E., and Forchhammer, M.C. 2002. Synchronization of animal population dynamics by large-scale climate. *Nature (London)*, **420**(6912): 168–171. doi:10.1038/nature01064. PMID:12432390.
- R Development Core Team. 2008. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. Available at <http://www.r-project.org>.
- Rao, C.R. 1964. The use and interpretation of principal component analysis in applied research. *Sankhya Ser. A*, **26**: 329–358.
- Reynolds, C.S. 1987. Community organization in the freshwater plankton. In *Organization of communities: past and present*. Edited by J.H.R. Gee and P.S. Giller. Blackwell Scientific Publishers, Oxford, UK. pp. 297–325.
- Sousa, W.P. 1979. Experimental investigations of disturbance and ecological succession in a rocky intertidal algal community. *Ecol. Monogr.* **49**(3): 227–254. doi:10.2307/1942484.
- ter Braak, C.J.F. 1986. Canonical correspondence analysis: a new eigenvector technique for multivariate direct gradient analysis. *Ecology*, **67**(5): 1167–1179. doi:10.2307/1938672.
- ter Braak, C.J.F. 1987. The analysis of vegetation–environment relationships by canonical correspondence analysis. *Vegetatio*, **69**(1–3): 69–77. doi:10.1007/BF00038688.
- ter Braak, C.J.F. 1988a. CANOCO — an extension of DECORANA to analyze species–environment relationships. *Vegetatio*, **75**: 159–160.
- ter Braak, C.J.F. 1988b. CANOCO — a FORTRAN program for canonical community ordination by [partial] [detrended] [canonical] correspondence analysis, principal components analysis and redundancy analysis. Version 2.1. Agricultural Mathematics Group, Wageningen, the Netherlands.
- Thrush, S.F., Schneider, D.C., Legendre, P., Whitlatch, R.B., Dayton, P.K., Hewitt, J.E., Hines, A.H., Cummings, V.J., Lawrie, S.M., Grant, J., Pridmore, R.D., Turner, S.J., and McArdle, B.H. 1997. Scaling-up from experiments to complex ecological systems: where to next? *J. Exp. Mar. Biol. Ecol.* **216**(1–2): 243–254. doi:10.1016/S0022-0981(97)00099-3.
- Vanderploeg, H.A., and Scavia, D. 1979. Two electivity indices for feeding with special reference to zooplankton grazing. *J. Fish. Res. Board Can.* **36**: 362–365.
- Wanink, J.H., and Witte, F. 2000. The use of perturbation as a natural experiment: effects of predator introduction on the community structure of zooplanktivorous fish in Lake Victoria. *Adv. Ecol. Res.* **31**: 553–570. doi:10.1016/S0065-2504(00)31030-3.
- Ward, J.V. 1998. Riverine landscapes: biodiversity patterns, disturbance regimes, and aquatic conservation. *Biol. Conserv.* **83**(3): 269–278. doi:10.1016/S0006-3207(97)00083-9.
- Whittaker, R.J. 1995. Disturbed island ecology. *Trends Ecol. Evol.* **10**(10): 421–425. doi:10.1016/S0169-5347(00)89164-8.
- Wilson, S.D., and Keddy, P.A. 1986. Measuring diffuse competition along an environmental gradient: results from a shoreline

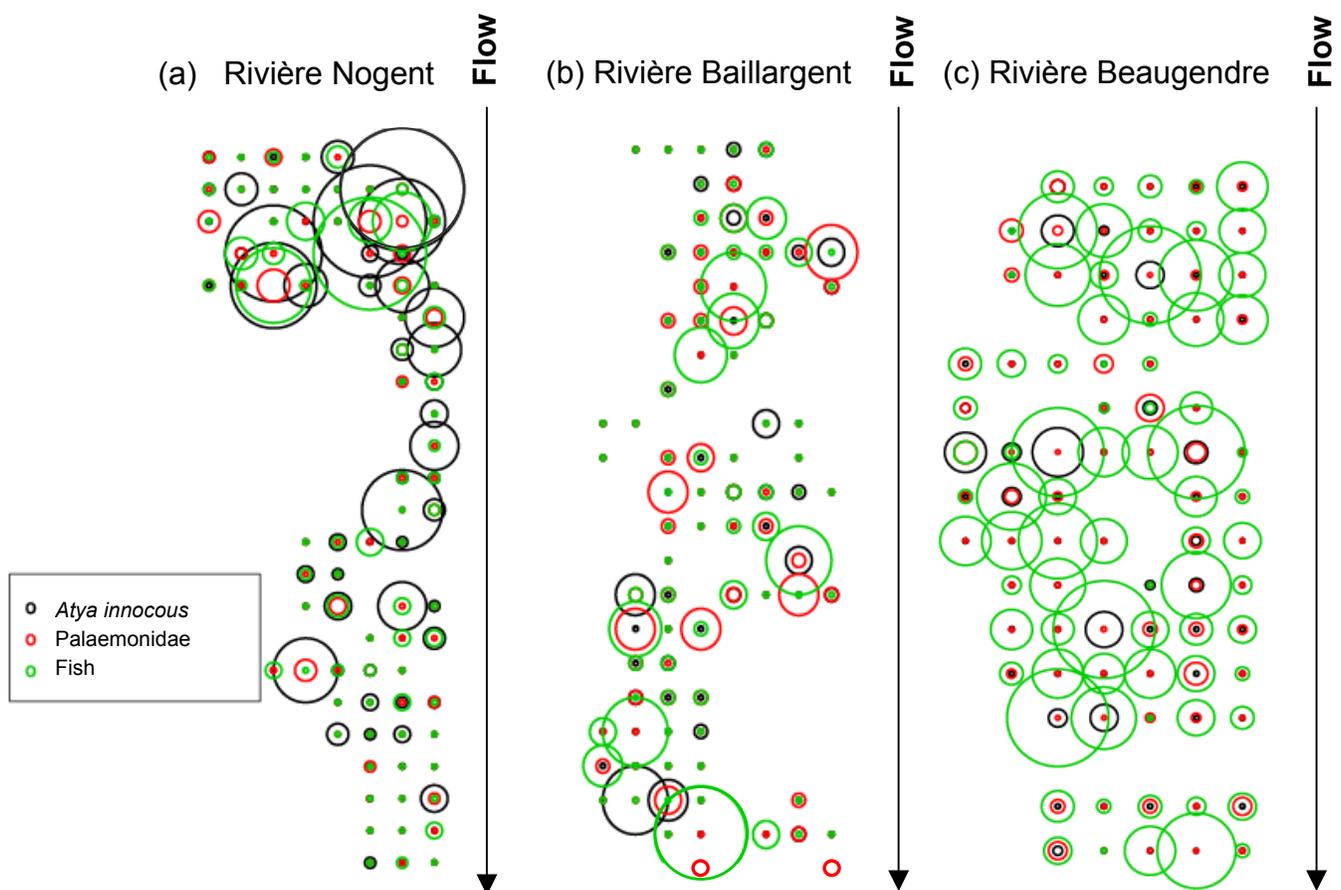
- plant community. *Am. Nat.* **127**(6): 862–869. doi:10.1086/284530.
- Winemiller, K.O., and Ponwith, B.J. 1998. Comparative ecology of eleotrid fishes in Central American coastal streams. *Environ. Biol. Fishes*, **53**(4): 373–384. doi:10.1023/A:1007422821071.
- Wright, M.S., and Covich, A.P. 2005. Relative importance of bacteria and fungi in a tropical headwater stream: leaf decomposition and invertebrate feeding preference. *Microb. Ecol.* **49**(4): 536–546. doi:10.1007/s00248-004-0052-4. PMID:16052374.

Monti, D. and Legendre, P. 2009. Shifts between biotic and physical driving forces of species organization under natural disturbance regimes. CJFAS.

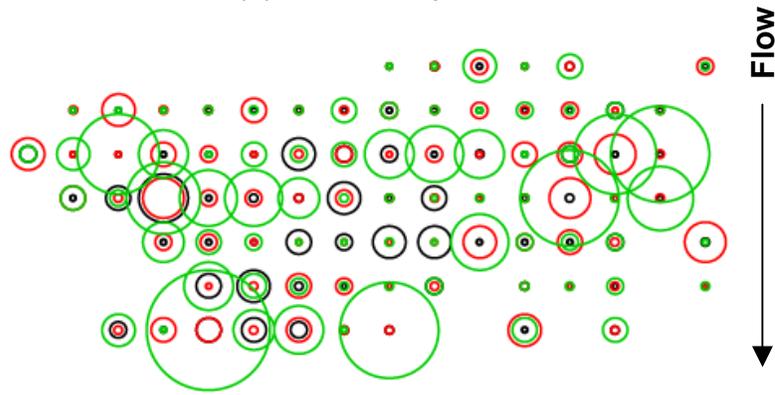
Supplemental Appendix S1

This Appendix shows the systematic design of the sampling conducted in the six rivers for the study of *Atya innocous* microdistribution and the spatially referenced abundances of *Atya* and co-occurring taxa (*Palaemonidae* crustaceans and fish). The spacing between quadrat centers is 2 m.

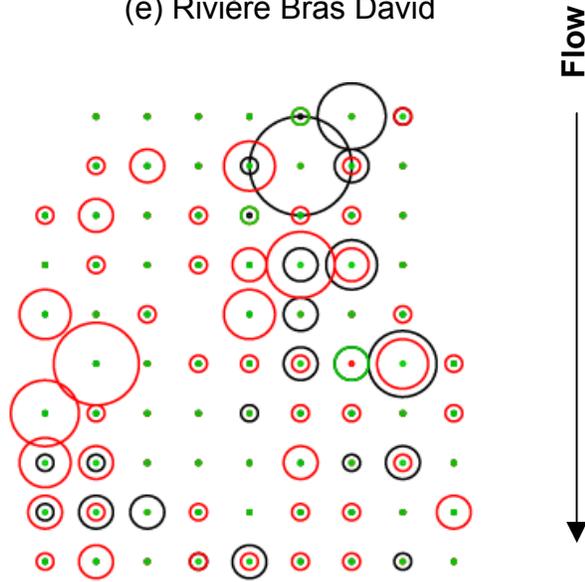
Fig. S1. Maps of the sampling quadrats in the six river reaches. Abundances are proportional to circle diameter.



(d) Rivière Capesterre



(e) Rivière Bras David



(f) Rivière de Vieux Habitants

