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Hydraulic preferences of shrimps and fishes in tropical insular rivers

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Short title: Hydraulic preferences of diadromous species

Key words: micro-habitat preferences; generalized additive models; transferability; Caribbean; Indian Ocean

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ABSTRACT

Hydraulic habitat models based on the preferences of species for the hydraulic characteristics of their microhabitats are frequently used to evaluate the impact on the habitat of a change in river flow regime. Their application in a tropical insular environment is still limited as little is known about the hydraulic preferences of species. Hydraulic preferences models have been developed for 15 taxa (diadromous shrimps and fishes) sampled in 52 rivers in the Caribbean (the French West Indies) and the Indian Ocean (the Reunion island). Five datasets were used and group 8353 samples collected by electrofishing during 320 surveys (reach×date) performed between 1999 and 2011. Generalised additive models were used to link variations of taxa density within surveys to the hydraulic characteristics of the microhabitat (velocity, depth, substrate). Hydraulic preferences within each region (Caribbean and Indian Ocean) are significant for most of the taxa and vary little between rivers and surveys. The hydraulic variables explain up to 18.1% (univariate models) and 30.0% (multivariate models) of the deviance of densities within survey. Of the taxa selected, *Atya scabra*, *Macrobrachium heterochirus*, *Xiphocaris elongata* and the Sicydiinae are the most demanding.

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INTRODUCTION

Tropical insular rivers are characterised by extreme and unpredictable hydrological events (typhoons, cyclones, Tew *et al.,* 2002) that alternate with sometimes severe periods of low flow (Covich, 2006) that are decisive for aquatic communities (Poff and Ward, 1989). The communities of these rivers are characterised by low density and are mainly composed of three families of shrimp (Atyidae, Palaemonidae, Xiphocaridae) and four families of fish (Eleotridae, Gobiidae, Mugilidae and Anguillidae) (Covich and McDowell, 1996), all of which are diadromous (McDowall, 2004). The catadromous species (Mugilidae, Anguillidae) spend their lives in rivers and reach the sea and/or river outlets to reproduce. Amphidromous species (Atyidae, Palaemonidae, Xiphocaridae, Gobiidae) spawn and grow in freshwater except during larval stages which require a saline environment. The complex lifecycle of these species makes them especially vulnerable to increasing demographic pressure (Mittermeier *et al.,* 2005; Smith *et al.,* 2008), such as dams that modify flow regimes and river habitats, and impede their migrations (March *et al.,* 2003; Milton, 2009). Many aspects of the flow regime may affect the habitats and the life cycle of tropical species (e.g. Welcomme and Halls, 2004). For example, the timing and the amplitude of floods may trigger fauna migration and reproduction (e.g. Way *et al.*, 1998; Blanco and Scatena, 2005; Kikkert *et al.*, 2009). However, little is known about the ecological impact of changes in low to moderate flows (Pringle *et al.,* 2000; Monti and Legendre, 2009).

Hydraulic habitat models have been used widely around the world to facilitate the management of low to medium discharges (Tharme 2003; Conallin *et al.,* 2010). This method uses models that predict the amount of favourable habitat at the reach scale (~10^2-10^3 m^2) as a function of discharge rate (Bovee, 1982; Ginot, 1995). Habitat models combine the hydraulic model of a stream reach with models of hydraulic preferences. Classically, hydraulic

preference models represent how the abundance or occurrence of a taxon (e.g. guild of species, species, life stage of a species) varies within the reach as a function of microhabitat parameters (e.g. velocity, depth, substrate). The applicability of habitat models is generally limited by their degree of transferability between rivers (Jowett, 2003; Lamouroux *et al.*, 2010; Lancaster and Downes, 2010). Indeed, habitat preferences can vary as a function of a large number of biotic and abiotic factors such as competition, predation, and water chemistry (Jackson *et al.*, 2001). In order to better quantify the generality of hydraulic preference models, it is therefore interesting to study the hydraulic preferences of taxa using data collected from different rivers at different times (seasons, years) (Leftwich *et al.*, 1997; Lamouroux *et al.*, 1999a; Strakosh *et al.*, 2003; Vilizzi *et al.*, 2004; Dolédec *et al.*, 2007; Mérigoux *et al.*, 2009). The models developed at several sites have led to contrasting conclusions, but have often highlighted the pertinence of models defined for a number of rivers sharing the same hydromorphological characteristics (Lamouroux *et al.*, 1999b; Lamouroux *et al. in press*).

Not much is known about the hydraulic preferences of tropical river species (Pringle *et al.*, 2000; Scatena, 2004; Boulton *et al.*, 2008). Research into these species has mainly focused on (1) the altitudinal distribution of species and the importance of maintaining upstream/downstream connectivity (Holmquist *et al.*, 1998), (2) trophic links and the role of macro-consumers (Crowl *et al.*, 2006; Coat *et al.*, 2009), (3) the effects of extreme events on population structures (e.g. the harmful effect of low water levels on the abundance of *Macrobrachium sp*., Covich *et al.*, 2006) and (4) the mechanisms and role of dispersion in population renewal (Keith *et al.* 2008; Crook *et al.*, 2009). However, few works have focused on the role of hydraulic constraints (e.g. shift of driving force under natural disturbance, Monti and Legendre, 2009) and the habitat selection mechanisms at the reach scale (e.g. habitat selection for Sicydiinae, Teichert *et al. in press*).

In this study, we examine how the density of 15 taxa of the families of Atyidae, Palaemonidae, Xiphocaridae, Gobiidae and Mugilidae vary as a function of the hydraulic parameters of the microhabitat (velocity, depth, substrate). The datasets used come from two regions: the French West Indies (Martinique, Guadeloupe) in the Caribbean and the island of Reunion in the Indian Ocean. These are recent volcanic islands with comparable hydromorphological characteristics (narrow valleys, abrupt reliefs, high waterfalls) (Falkland, 1992). Our main objectives were to (1) build hydraulic preference models for different taxonomic groups in each of the two regions (Caribbean, Indian Ocean), (2) estimate the transferability of models among datasets and groups of surveys, and (3) compare hydraulic preferences among the species of the same family.

METHODS

Reaches and sampling dates

We used five datasets (Table 1), three collected from the Caribbean and two from the Indian Ocean (Figure 1). Abundance samples were taken in 121 reaches of 52 rivers during periods of 1 to 12 years. The reaches were distributed over the entire island, in river sections with persistent flows, and were sometimes located upstream or downstream of water intakes. The length of the reaches varied from 0.05 to 2.75 km so that each reach encompassed a variety of morphological units (e.g. riffles, rapids, pools, cascades). The reaches were located at an altitude between 5 and 670 m, at a distance from the sea from 0.1 to 22.8 km and at a distance of 1 to 34.5 km from the source. The surface area of the watersheds upstream of the reach was on average (± standard deviation) 15 (± 15 km^2) in the Caribbean and 70 (± 49 km^2) in the Indian Ocean. Most of the sampling was performed during the low flow period (when hydraulic selection occurs), i.e. from December to May in the Caribbean (Chaperon *et al.*, 1983) and from November to April in the Indian Ocean (Robert, 1988). 20% of the surveys

(reach×date) in the Caribbean were carried out during the high flow period but when discharge rate was relatively low.

Sampling methods

Sampling of fishes and shrimps was done by electrofishing using three methods (Table 1) according to the objectives of previous studies (e.g. analysis of spatial patterns, Monti and Legendre, 2009). The "points" method consisted in collecting 50 samples (~ 1 m^2) distributed randomly in the reach by positioning a portable electrode (e.g. DEKA 3000 Lord; DEKA-Gerätebau, Marsberg, Germany) without moving it (Fiévet *et al.*, 1996). The "habitat units" method consisted in fishing about 20 samples from wider surface areas distributed in the available morphological units. The surface area of the samples was 17 m^2 on average (± 8 m^2). The "quadrats" method consisted in fishing about 90 contiguous samples (squares of surface area = 4 m^2) in the reaches. These different methods have been used by different teams and were not intercalibrated in our reaches. However, point samples and habitat unit samples have already been combined in habitat modelling. For example, Lamouroux *et al.* (1999b) predicted fish density differences between reaches sampled by points from preference models made in other reaches sampled by habitat units.

Each sample was characterised by three microhabitat variables: average velocity (v), average water depth (h) and the size of the substrate (d). v, h and d were estimated on the basis of measurements along one vertical (44% of cases) or several verticals distributed in the sampling area (56% of cases). On each vertical, point velocities were measured using a current meter (a propeller for dataset Gq; an electromagnetic current meter for the other datasets) at 0.2h, 0.4h and 0.8h at the bottom of the bed when h > 0.20 m, otherwise at 0.4h. However, 5.4% of the velocities were estimated at the water surface as a function of the distance travelled by a float over a given time. The dominant substrate size d of the sample

area was estimated visually using ordinal classes (Cailleux 1954; Malavoi and Souchon, 1989). The central value of the class of substrate was assigned to *d*.

Each individual fish was measured and identified at species level (Keith *et al.*, 1999, Lim *et al.*, 2002, Monti *et al.*, 2010), except for three taxa in the Caribbean (Table 1): *Sicydium sp.* groups two species of fish, *Sicydium punctatum* and *Sicydium plumeri*, of the Gobiidae family (subfamily Sicydiinae); *Atya sp.* groups the juvenile shrimps of *Atya scabra* et *Atya innocous*; and *Macrobrachium sp.* groups the juvenile shrimps of the family of Palaemonidae (subfamily *Macrobrachium*). However, the individuals of dataset Gq (Table 1) were not measured.

Taxa selected

Of the 21 to 28 species sampled in each dataset (Table 1) only the taxa with a total abundance > 200 individuals were chosen for the analysis. Therefore, we selected 11 taxa in the Caribbean belonging to three families of shrimp (Atyidae, Xiphocariidae, Palaemonidae) and two families of fish (Mugilidae, Gobiidae), and four taxa in the Indian Ocean belonging to two families of shrimp (Atyidae, Palaemonidae) and one family of fish (Gobiidae) (Table 2). In order to get round the problem of different surface areas of the samples used in the analyses, the abundances of the samples were transformed to densities (Ď, number of each for an equivalent surface of 10 m^2). Taxa size classes were defined in order to infer the effect of size preferences on hydraulic. The limits of classes were chosen to obtain comparable numbers.

Statistical modelling

For each taxon of each region, we modelled the Ď as a function of microhabitat variables with a series of generalised additive models (GAMs). GAMs permit considering nonlinear relations, that are frequent when studying hydraulic preferences (e.g., Lamouroux *et al.*, 1999a; Jowett *et al.*, 2008). They have a flexible structure that does not require prior determination of the form of the relation (Guisan and Zimmerman, 2000, Guisan *et al.*, 2002). Six models (Eqs. 1-6) were defined with a log link function. The reference model M1 (Eq. 1) assumes that the density is constant by survey, so that there is no hydraulic preference. Model M2 (Eq. 2) defines the regional model where the abundance varies similarly in each survey as a function of a microhabitat variable. By comparing M2 in relation to M1, we quantify the strength of hydraulic preference independently of the other biotic and abiotic factors acting at the scale of the reach on a given date. In model M3 (Eq. 3), the hydraulic preferences can vary as a function of the dataset, i.e. the island or the sampling method. In model M4 (Eq. 4), the hydraulic preferences can vary as a function of the dataset and groups of surveys. The latter two models permit appreciating the transferability of the results between rivers. Different criteria were used to define two groups of surveys in M4 (with comparable numbers): the season of low and high flow in the Caribbean; the years < and ≥ 2009 in the Caribbean and the years < and ≥ 2005 in the Indian Ocean; the altitude (≤ or > 165 m in the Caribbean; < and ≥ 80 m in the Indian Ocean); the wind coast exposure (exposed or not); the size of the watershed (≤ or > 10 km^2 in the Caribbean; ≤ or > 50 km^2 in the Indian Ocean); the situation in relation to water intakes (upstream of an intake or not; only in the Caribbean). Lastly, models M5 and M6 (Eqs. 5-6) define multivariate models for a taxon with or without a term of interaction between microhabitat variables. Concerning the preference models of taxa size classes, we fitted M1 and M2 only. Our series of models is:

M1: $\log(\check{D}) \sim a_{survey}$ (1)

M2: $\log(\check{D}) \sim a_{survey} + s(p)$ (2)

M3: $\log(\check{D}) \sim a_{survey} + s(p) + s(p{:}p_{dataset})$ (3)

M4: $\log(\check{D}) \sim a_{survey} + s(p) + s(p{:}\ p_{dataset}) + s(p{:}p_{survey})$ (4)

M5: $\log(\check{D}) \sim a_{survey} + s(v) + s(h) + s(d)$ (5)

M6: $\log(\check{D}) \sim a_{survey} + s(v) + s(h) + s(d) + s(v, h, d)$ (6)

where p corresponds either to *v*, *h* or *d*; s() is a smoothing function (of cubic spline type); $p{:}p_{dataset}$ is the term of interaction between the hydraulic variable and the *dataset* variable; $p{:}p_{survey}$ is the term of interaction between the hydraulic variable and a group of surveys. The parameter a_{survey} permits ignoring differences in density between surveys which do not reflect the microhabitat hydraulic preferences.

For all the models, we chose a negative binomial (NB) type error distribution, which can account for the over-dispersion of abundance data, as suggested by Gray *et al.* (2005, freshwater macro-invertebrates) and Vaudor *et al.* (2009, freshwater fishes) for data of the same type. We set the dispersion parameter (θ) of the NB distribution for each taxon when fitting model M1. We also set the degree of freedom of the smoothing function of the GAMs at three to avoid any over-parameterisation (Jowett *et al.*, 2008). Lastly, for each taxon we eliminated the surveys where the number of individuals was less than three. The models were fitted using the functions available in the *mgcv* package (Wood, 2006) of the R software (R Development Core Team, 2010).

We described the quality of our two series of nested models (M1-M4 and M1, M5-M6) using the additional deviance explained in comparison to the previous model. In addition, we used a likelihood ratio test to compare a given model with the previous one.

RESULTS

A total of 8353 samples were collected from 320 surveys, making it possible to establish and study the preferences of 11 taxa and 16 size classes in the Caribbean, four taxa and eight size classes in the Indian Ocean (Table 2). The velocities of the samples varied from 0 to 2.80 $m.s^{-1}$, the depths from 0.02 to 1.90 m and the substrate from 0 to 1.024 m.

The dispersion parameter θ varied from 0.06 (*A. scabra*) to 0.46 (*M. poeyi*) for the taxa of the Caribbean, and from 0.32 (*A. serrata*) and 1.10 (*S. lagocephalus*) for the taxa of the Indian Ocean (Table 2, standard error on $\theta \leq 0.03$ for all species). The low values of θ, which indicate over-dispersion of densities, were obtained for rare species (*M. crenulatum*, *A. monticola*) and those known to be gregarious (*A. scabra*; Lim *et al.*, 2002; Monti *et al.*, 2010).

Univariate models M1 – M4 by taxon

The deviance explained by the survey in reference model M1 varied from 20.3 to 56.0% (on average 36%, Table 3). The addition of microhabitat variables in M2 explained from 0 to 18.1% (average 4.3%) of the residual deviance of M1. The model of velocity preferences was generally more efficient than that of preferences of depths and substrates (on average 6.9, 4.4 and 1.6% of explained deviance, respectively). Examples of fits of M2 models to the data observed are given in Figure 2.

Hydraulic preferences were significant for most of the species, except *A. monticola* (*v* and *d*), *M. crenulatum*, *Atya sp.* and *X. elongata* (*d*) (Table 3). The strongest preferences, relative to velocity and depth, concerned *A. Scabra*, *M. heterochirus*, *X. elongata* and *Sicydium sp.* in the Caribbean and *S. lagocephalus* and *C. acutipinnis* in the Indian Ocean. The taxa had preferences for low (*X. elongata, M. crenulatum, M. faustinum, M. australe*),

intermediate (*A. innocous*, *M. poeyi*) or high (*A. Scabra*, *M. heterochirus*, *A. serrata* and Sicydiinae) velocities, whereas most taxa preferred shallow depths, except *X. elongata*, *M. crenulatum* and *M. australe* (Figures 3 and 4). *A. scabra*, *M. heterochirus*, *A. serrata*, *C. acutipinnis* and *S. lagocephalus* preferred coarse substrates whereas *M. australe* preferred fine substrates (Figures 3 and 4).

The preferences for velocities and depths, and to a lesser extent substrates (Table 3), differed between datasets. However, the additional deviance explained by M3 in comparison to M2 remained low: it was < 2.2% in the Caribbean and < 1.5% in the Indian Ocean (Table 3). The main differences observed in the Caribbean are the variations of preferences in the range of high velocities (> 0.5 $m.s^{-1}$) (cf. *A. scabra* in Figure 3) and preferences for shallower or deeper water depths (cf. *A. monticola* in Figure 3). In the Indian Ocean, we observed preferences for lower velocities and an absence of preferences for depths in the dataset sampled by "points" in comparison to "habitat units" for *C. acutipinnis* (*v*, *h*) (Figure 4). Regarding variations between groups of surveys, the comparison of M4 and M3 indicated that the localisation parameters of reaches and the sampling period generally had little influence on hydraulic preferences (explained relative deviance < 2.4%, Table 3). The highest values observed concerned *A. scabra* in the Caribbean, and *A. serrata*, *M. australe* and *C. acutipinnis* in the Indian Ocean.

Univariate models M1 – M2 by size classes

The hydraulic preferences according to size classes were mostly significant except for the preferences of *X. elongata* (*h*), *A. monticola* (*h*) and *A. serrata* (*d*) of small sizes and the preferences of adults of *Sicydium sp*. (*d*) and *A. monticola* (*v*) (Table 4, Figure 5). The deviance explained by the models by size classes was close to that of the model by taxon. The deviance explained was nonetheless higher for size classes concerning the preferences for

substrate. The preferences of larger individuals for velocities were weaker than those of smaller individuals for the species *A. scabra* and *X. elongata*; on the contrary, the preferences of larger individuals for velocities were stronger than those of smaller individuals for the species *Sicydium sp.*. Size classes generally preferred similar depth ranges except for the taxa *X. elongata,* where larger individuals tended to prefer deeper habitats (Figure 5). The preferences of larger individuals for substrate are weaker than those of smaller individuals for *M. australe* and *M. heterochirus*; conversely, larger individuals of *A. scabra*, *A. serrata* and *S. lagocephalus* have stronger preferences for substrate.

Multivariate models M5 – M6

The multivariate models without interactions (M5) explained from 2.8 to 24.4% of the residual deviance of M1 (Table 5). The addition of an interaction term (M6) improved the explained deviance between 3.7 and 9.4% for some taxa: *Sicydium sp.*, *X. elongata*, *C. acutipinnis* and *S. lagocephalus* (Table 5).

DISCUSSION

The within-survey deviance explained by microhabitat variables varies between 0 and 18.1% (univariate regional models) and from 4.1 to 30.0% (multivariate regional models). The poor performances achieved by the models built are partly due to the small size of the scale of observation (~ 1 m^2) and likely result from the particular life cycle of the taxa (diadromous and opportunistic species). Similarly, the within-survey deviance of models of hydraulic preferences of the white shrimp *Paranephrops planifrons*, a diadromous species of the rivers of the north island of New Zealand, varies from 7 and 11% (Jowett *et al.*, 2008). By way of

comparison, Dolédec *et al.* (2007) showed that models of European regional preferences for macro-invertebrates explained on average 25% of within-survey variance.

Taxa showing the most marked hydraulic preferences are *A. scabra*, *M. heterochirus*, *X. elongata*, *Sicydium sp.* in the Caribbean, and *C. acutipinnis* and *S. lagocephalus* in the Indian Ocean. For example, the density of *A. scabra* and *X. elongata* can be multiplied by a factor of ~ 5 for a change of velocity in the order of 0.5 $m.s^{-1}$.

The preferences of shrimps for high (*A. scabra*, *M. heterochirus*) or low (*X. elongata*) velocities are probably linked to their capacity to resist currents or not and their foraging strategy. Indeed, *A. scabra* and *M. heterochirus* are larger in comparison to the other species of the same family (*M. poeyi*, *M. faustinum*) and have larger morphological attributes (pincers, legs, spines on pincers) (Lim *et al.*, 2002) that allow them to move in rapids where densities of drifting benthos, particles and/or individuals are higher (Orth and Maughan, 1983; Brooks *et al.*, 2005). Furthermore, the feeding mode of *A. scabra* is probably more specialised than for *A. innocous*, likewise with *M. heterochirus* in comparison to *M. crenulatum*. On the contrary, *X. elongata* has a strong preference for low velocities and deeper water since it lives essentially in the water column (Lim *et al.*, 2002). In addition, our results corroborate those of Monti and Legendre (2009) who showed that *M. heterochirus* and *X. elongata* have notable preferences for velocities in environments with strong hydrological disturbances.

The fish of the subfamily of Sicydiinae in the two regions (*Sicydium sp.*, *C. acutipinnis* and *S. lagocephalus*) prefer fast-flowing and shallow habitats. Their hydraulic preferences are probably linked to the presence of periphytic biofilm whose quality and development are conditioned by bed shear stress and light, respectively (Julius *et al.*, 2005; Lefrançois *et al.*, 2011; Tabouret *et al.*, 2011). The hydraulic preferences of *S. lagocephalus* and *C. acutipinnis* are comparable to those given by the logistic models built by Teichert *et al.* (*in press*), except that the authors showed that *C. acutipinnis* has stronger preferences for

depths than velocities. This difference in preference strength can be due to the longer sampling period covered by our dataset.

Taxa showing weaker hydraulic preferences are *A. monticola*, *M. faustinum*, *M. crenulatum*, *M. australe*, *A. innocous*, *M. poeyi* and the juvenile shrimps of the Caribbean. These results are consistent with those of Monti and Legendre (2009) who reported weak preferences for velocity for *M. faustinum* and *M. poeyi*. Concerning *M. crenulatum,* Monti and Legendre identified strong preferences for low velocities for four sites under strong and weak hydrological disturbance, suggesting that food predominates in influencing habitat selection. Some of these species are also described with preference variables according to diurnal phases (e.g. *A. innocous)* (Keith *et al.,* 1999; Lim *et al.,* 2002; Monti *et al.,* 2010). The weak preferences of the species observed here can also be partly due to variations in fishing efficiency or to our grouping of juveniles of some taxa (*A. scabra* and *A. innocous*; *M. crenulatum*, *M. heterochirus* and *M. faustinum*). Regarding fishing efficiency, it is as poor as the species are rare (*M. crenulatum*) and their mobility is high (*A. monticola*) (Fiévet *et al.,* 1999; King *et al.,* 2002). It is therefore possible that fishing efficiency explains the absence of preference for velocity that we observed for the mobile *A. monticola,* whereas the taxon is expected to prefer fast and well oxygenated water (Lim *et al.,* 2002). Fishing efficiency can also explain that we observed weak preferences for *A. innocous*, which is an excellent swimmer and very reactive in the presence of predators (Covich *et al.,* 2009; Hein and Crowl, 2010) or when disturbed by electrofishing (Fiévet *et al.,* 1999). Regarding the shrimp *M. australe*, its weak regional preferences can be explained by its sheltering behaviour during the day and variation due to its morphological plasticity (Zimmermann *et al.,* 2012). The grouping of juveniles of different species of *Macrobrachium* is probably not very appropriate since we observed that the adults of *M. faustinum* and *M. heterochirus* have different preferences (forces and directions) regarding velocity and depth. This is less the case for the juveniles of the family of Atyidae since the adults (*A. scabra*, *A. innocous* and *M. poeyi*) share

relatively similar preferences. Lastly, the more flexible mode of feeding (filtering and scraping) of *M. poeyi* and *A. innocous* in comparison to *A. scabra* (mainly filtering) can also explain less selective use of microhabitats.

The comparison of inter-species hydraulic preferences suggests that food strategies (filtering and/or scraping) and morphological adaptations (size, apical spine) effectively influence habitat selection. This result supports that aquatic taxa have developed strategies shaped by the flow regime (Poff and Ward, 1989; Poff, 1997). The use of life history traits is therefore encouraged for overcoming problems of identification and/or lack of data on a particular species (Blanck *et al.*, 2007).

The low additional deviance explained by datasets or groups of surveys suggests that regional models are pertinent for expressing taxa preferences. Likewise, the performance of models regarding size class does not suggest a notable improvement. These results should nonetheless be seen relatively. For example, it is possible that our definitions of groups are not very appropriate for expressing different competition conditions. These effects can exist for certain species (*S. lagocephalus* and *C. acutipinnis*, Lord *et al.*, 2011) and might partially explain the variations observed between groups in our results (*C. acutipinnis*). Likewise, taking the hydrological regime (Monti and Legendre, 2009) into account in more detail would undoubtedly lead to more thorough models. Lastly, a breakdown of taxa by life stage rather than by size class could be more pertinent to reflect the physiological needs of species (Bielsa *et al.*, 2003, for *S. lagocephalus*) and their behaviours regarding different predators (e.g. longer rostrum in *X. elongata* in the presence of predatory fish, Covich *et al.*, 2009).

To sum up, the hydraulic preferences of insular tropical taxa are generally weaker than in temperate regions. This observation, as well as the complexity of the life cycle of these taxa, tends to emphasise that the hydraulic preferences of taxa should only be taken into account

within an approach that provides a more general description of their habitat during their life cycle. This approach would imply in particular taking into account the ecological effect of various flow regime attributes (e.g., timing and duration of floods, flashiness; Bunn and Arthington, 2002), the longitudinal connectivity (e.g., Greathouse *et al.*, 2006) and the potential threat of introduced species (Donlan and Wilcox, 2008). Nonetheless, our results show that the hydraulic preferences of certain taxa are significant (e.g., *A. scabra*, *M. heterochirus*) and consistent with the knowledge available on these taxa. Our regional models can contribute to describe the hydraulic preferences of these taxa and model how the management of low to average discharges modifies their available habitat.

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Table 1: Datasets characteristics

Dataset code	Island	Sampling method	Number of surveys	Number of samples (min-max per station)	Sampling Years	Number of taxa sampled
Caribbean						
Gp	Guadeloupe	Points	32	1455 (10 - 52)	2005, 2008, 2009	23
Gq	Guadeloupe	Quadrats	27	1811 (79 - 99)	2005	22
Mp	Martinique	Points	21	946 (31 - 50)	2008, 2010	21
Indian Ocean						
Rp	Réunion	Points	17	1359 (13 - 85)	1999, 2001	25
Rh	Réunion	Habitat units	196	3284 (3 - 21)	2000-2011	28

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Table 2: Selected taxa and their main ecological characteristics. Habitat use and feeding groups are summarized from information detailed in Coat *et al.* (2009, 2011), Keith *et al.* (1999), Lim *et al.* (2002) and Monti *et al.* (2010). Abbreviations for feeding guilds are: F for filter feeding, H for Herbivore, D for Detritivore, O for Omnivore. θ (σ_θ) is the dispersion coefficient (and its standard error) fitted for the taxa.

Taxa Code	Taxa	Family	Habitat use	Feeding group	Number of occurrence in sample	Number of individuals	θ	σ_θ	Mean size (mm)
Caribbean									
AIN	*Atya innocous (Herbst, 1972)*	Atyidae	Rapid	F, D/H	1139	8873	0.22	0.01	47
ASC	*Atya scabra (Leach, 1815)*	Atyidae	Rapid	F, D/H	391	1556	0.06	0.00	51
ASP	*Atya sp. (juvenile)*	Atyidae			560	2135	0.09	0.00	
MPO	*Micratya poeyi (Guérin-Méneville, 1885)*	Atyidae	Vegetation	F, D/H	2407	25759	0.46	0.01	18
XEL	*Xiphocaris elongata (Guérin-Méneville, 1855)*	Xiphocariidae	Pool, river banks	D/H	956	5513	0.11	0.00	44
MCR	*Macrobrachium crenulatum (Holthuis, 1950)*	Palaemonidae	Rapid, deep run	O	345	565	0.06	0.00	57
MFA	*Macrobrachium faustinum (de Saussure, 1857)*	Palaemonidae	Pool, shelter	O	1814	5657	0.34	0.01	42
MHE	*Macrobrachium heterochirus (Wiegmann, 1836)*	Palaemonidae	Rapid	O	1010	1793	0.14	0.01	48
MSP	*Macrobrachium sp. (juvenile)*	Palaemonidae			1147	2984	0.17	0.01	
AMO	*Agonostomus monticola (Bancroft, 1834)*	Mugilidae	Rapid	D/H	307	617	0.06	0.00	124
SIC	*Sicydium sp. (Perugia, 1986; Bloch, 1786)*	Gobiidae	Rapid	H	2208	11658	0.32	0.01	50
Indian Ocean									
ATY	*Atyoida serrata (Bate, 1888)*	Atyidae	Rapid, vegetation	F, D/H	532	2974	0.32	0.01	18
MAA	*Macrobrachium australe (Guérin-Méneville, 1838)*	Palaemonidae	Pool	O	476	1444	0.51	0.02	42
COA	*Cotylopus acutipinnis (Guichenot, 1863)*	Gobiidae	Rapid	H	1033	2719	0.92	0.03	44
SLA	*Sicyopterus lagocephalus (Pallas, 1770)*	Gobiidae	Rapid	H	2423	11512	1.10	0.03	60

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Table 3: Explained deviance for M1 (% of the initial deviance) and supplementary deviance M_i/M_{i-1} (% of the residual deviance of M_{i-1} explained by M_i). Additional deviance is shown for significant cases only (P-value <0.05).

	Taxon	M1	Hydraulic parameter	M2/M1	M3/M2	M4/M3				
						Altitude	With-drawals	Coast exposure	Basin surface area	years
Caribbean	AIN	52.4	v	2.8	-	-	-	-	-	-
			h	1.2	0.5	0.4	-	-	-	-
			d	0.4	0.6	-	-	-	-	0.4
	AMO	20.3	v	-	-	-	-	-	-	-
			h	4.0	2.2	0.6	-	-	-	-
			d	-	-	-	-	-	-	-
	ASC	30.7	v	18.1	1.5	-	-	0.8	-	-
			h	5.4	0.9	2.2	1.1	2.0	1.2	1.2
			d	3.9	-	-	-	-	-	-
	ASP	20.9	v	1.9	-	-	-	-	0.5	-
			h	2.6	0.9	0.7	1.0	-	0.4	-
			d	-	1.2	-	-	-	0.5	-
	MCR	32.3	v	3.1	-	-	-	0.7	-	-
			h	0.5	-	-	-	-	-	-
			d	-	0.8	-	-	-	-	-
	MFA	30.9	v	1.6	0.3	-	0.6	0.1	0.5	-
			h	0.9	-	0.4	0.2	-	0.4	-
			d	0.5	-	-	-	-	0.2	-
	MHE	24.3	v	7.1	0.7	-	-	-	-	-
			h	1.5	0.8	-	-	0.4	0.6	0.3
			d	1.0	0.4	-	0.2	0.3	-	0.3
	MPO	45.0	v	3.3	0.3	0.2	-	-	0.2	-
			h	2.9	1.1	-	-	-	-	0.2
			d	0.9	0.4	0.6	-	-	-	-
	MSP	28.1	v	1.1	0.9	-	0.5	-	-	-
			h	1.7	0.5	-	0.2	0.3	0.3	0.5
			d	0.5	-	-	-	-	-	0.3
	SIC	33.2	v	3.8	0.5	0.1	-	0.2	0.3	0.1
			h	2.8	0.8	0.2	0.3	-	0.3	-
			d	0.3	-	-	-	-	0.1	-
	XEL	29.7	v	8.1	-	1.0	0.4	-	0.8	-
			h	2.4	0.7	0.4	-	0.4	-	-
			d	-	0.7	-	-	-	-	-
Indian Ocean	ATY	48.7	v	3.0	-	2.4		0.5	-	-
			h	5.6	-	0.4		-	0.8	0.6
			d	1.6	1.0	0.5		-	0.9	-
	COA	56.0	v	9.3	1.5	1.4		-	2.1	0.2
			h	5.3	1.5	1.3		-	-	-
			d	1.1	-	-		0.5	-	0.0
	MAA	44.4	v	5.4	-	-		0.3	1.9	2.4
			h	1.4	1.5	-		0.4	-	1.7
			d	3.0	0.9	-		1.3	-	0.0
	SLA	39.7	v	16.9	0.3	1.3		0.3	0.8	-
			h	13.5	0.9	1.6		0.5	1.1	-
			d	2.7	-	0.3		-	0.6	-

Table 4: Supplementary deviance M2/M1 (% of the residual deviance of M1 explained by M2) for size classes. Additional deviance is shown for significant cases only (P-value <0.05).

Region	Taxon	Size class (mm)	M2/M1		
			v	h	d
Caribbean	AIN	≤ 45	2.7	2.5	-
		> 45	2.4	1.2	-
	AMO	≤ 115	1.8	-	1.1
		> 115	-	7.7	1.3
	ASC	≤ 50	20.9	10.1	3.1
		> 50	16.9	3.2	5.2
	MCR	≤ 55	1.3	2.5	-
		> 55	2.8	1.7	-
	MFA	≤ 40	2.1	0.5	0.5
		> 40	3.0	1.6	0.6
	MHE	≤ 45	7.4	3.3	2.0
		> 45	6.0	1.4	0.9
	MPO	≤ 15	2.1	4.3	0.5
		> 15	3.2	4.5	0.8
	SIC	≤ 45	2.6	5.4	-
		> 45	5.5	2.5	0.5
	XEL	≤ 40	11.0	-	-
		> 40	8.8	2.5	-
Indian Ocean	ATY	≤ 20	3.1	6.0	-
		> 20	3.7	5.2	4.3
	COA	≤ 35	8.2	9.4	0.5
		> 35	8.5	4.1	1.3
	MAA	≤ 40	7.4	2.1	3.6
		> 40	3.8	1.4	1.2
	SLA	≤ 55	11.6	13.6	1.0
		> 55	16.2	9.7	3.7

Table 5: Explained deviance for M1 (% of the initial deviance) and supplementary deviance M_i/M_{i-1} (% of the residual deviance of M_{i-1} explained by M_i). Additional deviance is shown for significant cases only (P-value <0.05).

Region	Taxon	M1	M5/M1	M6/M5
Caribbean	AIN	52.4	3.8	1.4
	AMO	20.3	4.6	2.8
	ASC	30.7	23.7	0.9
	ASP	20.9	4.1	2.8
	MCR	32.3	3.3	1.5
	MFA	30.9	2.8	1.3
	MHE	24.3	8.3	1.0
	MPO	45.0	6.5	1.2
	MSP	28.1	3.3	2.7
	SIC	33.2	6.4	3.7
	XEL	29.7	10.1	5.3
Indian Ocean	ATY	48.7	9.2	1.7
	COA	56.0	11.0	9.4
	MAA	44.4	3.6	2.5
	SLA	39.7	24.4	5.7

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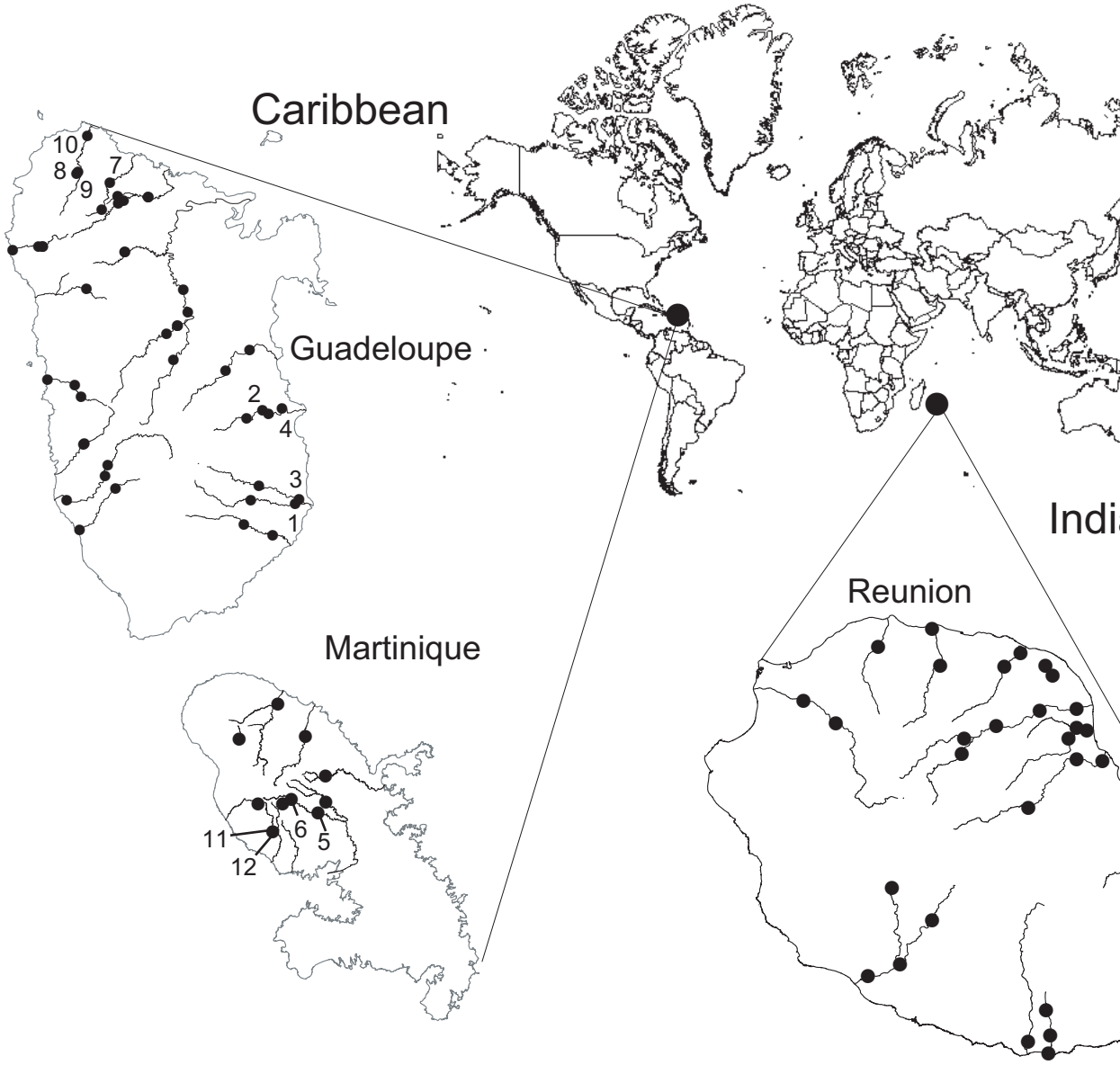

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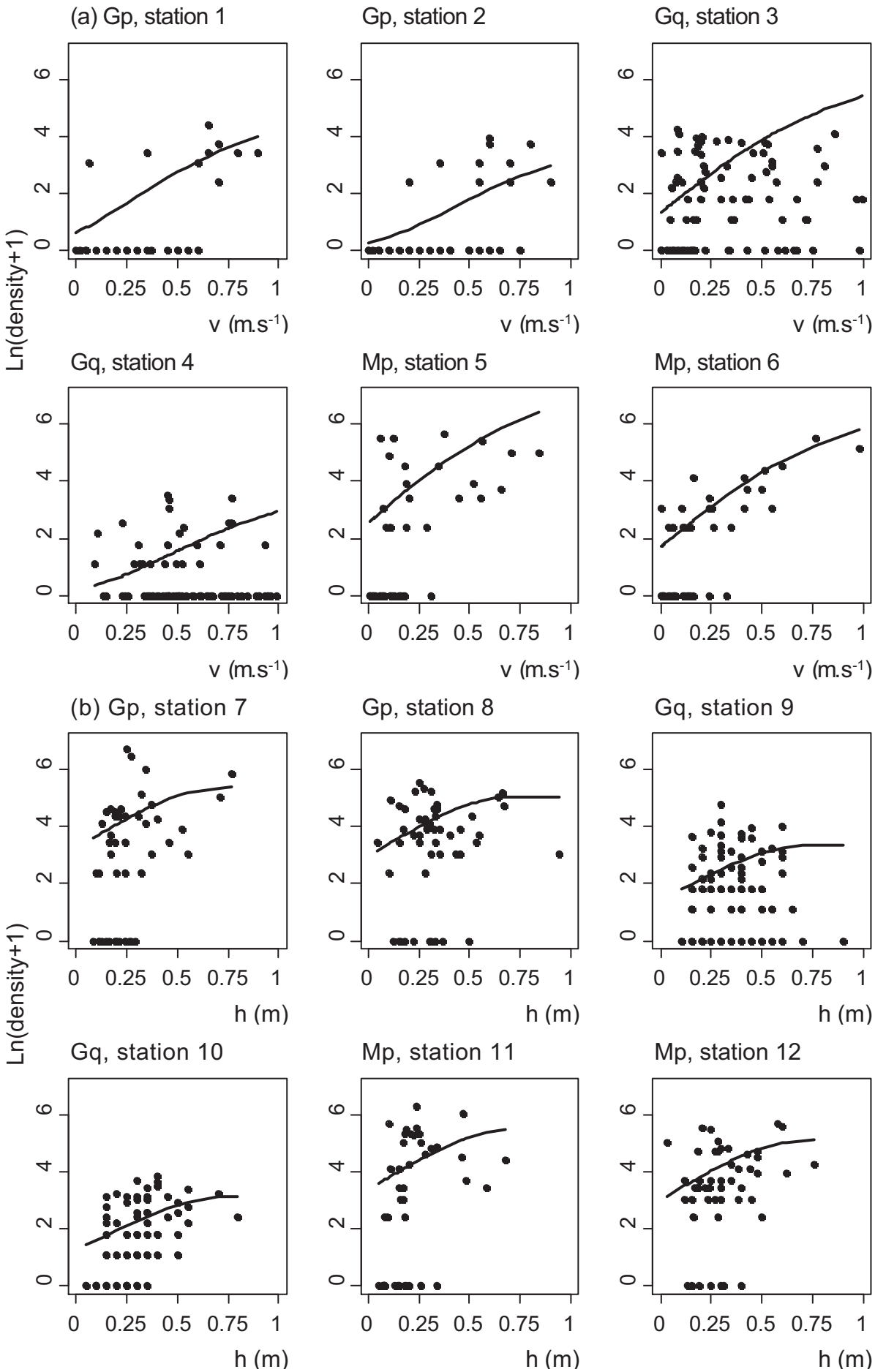

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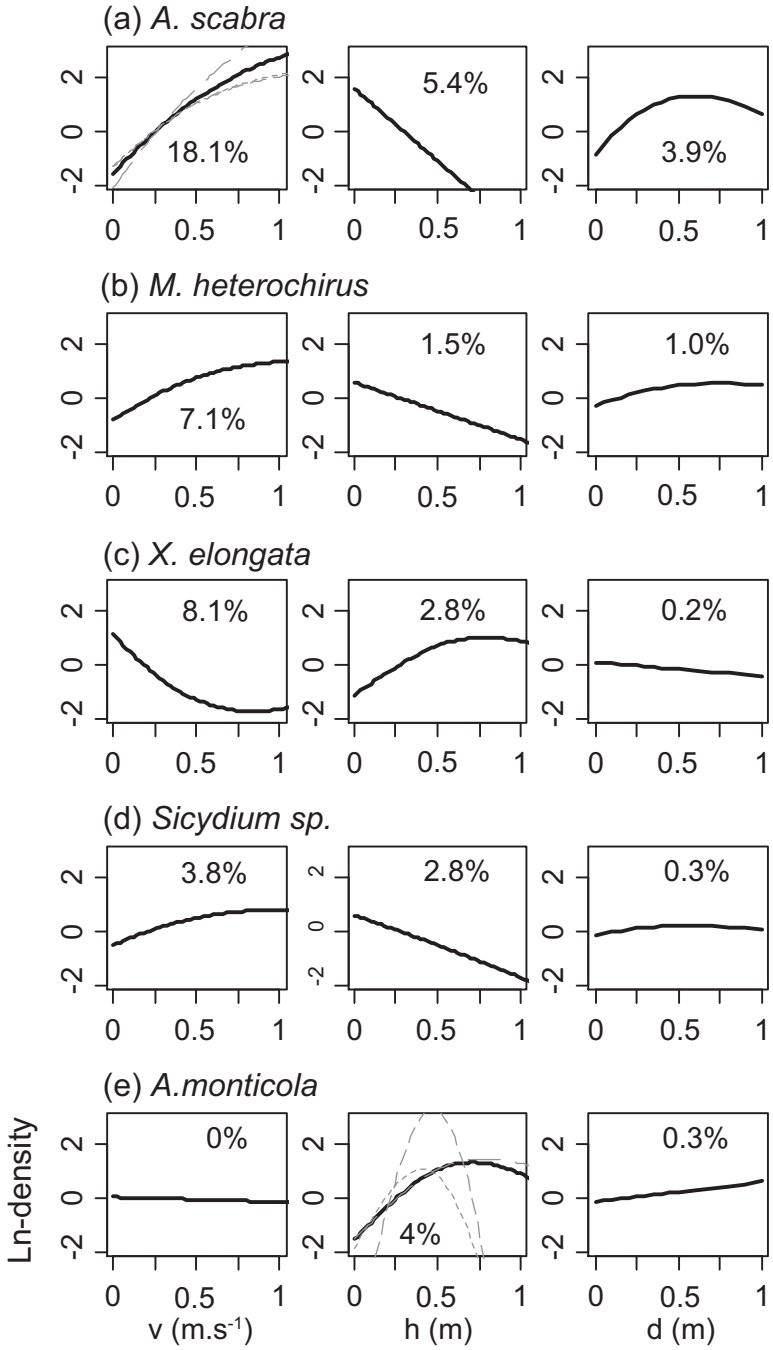

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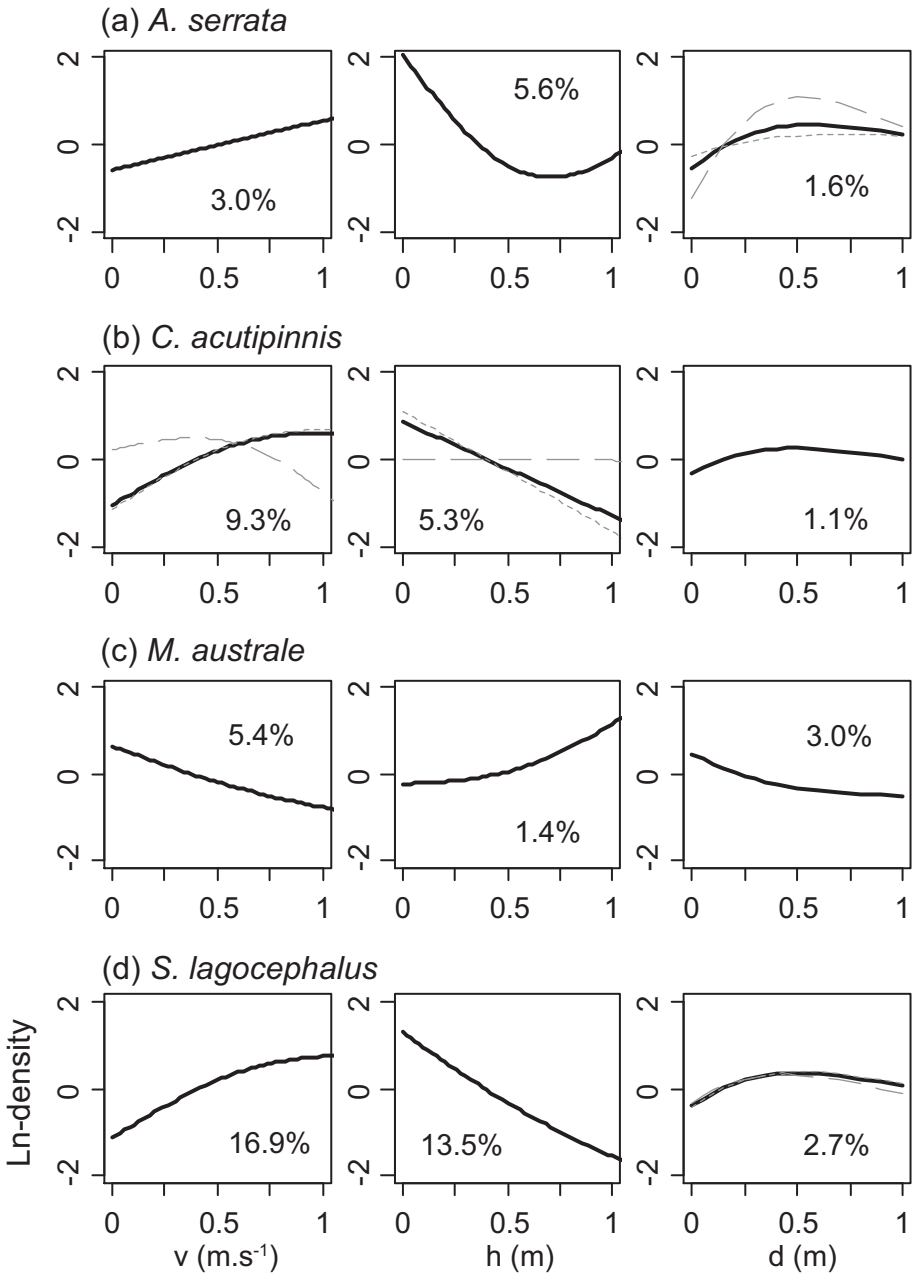
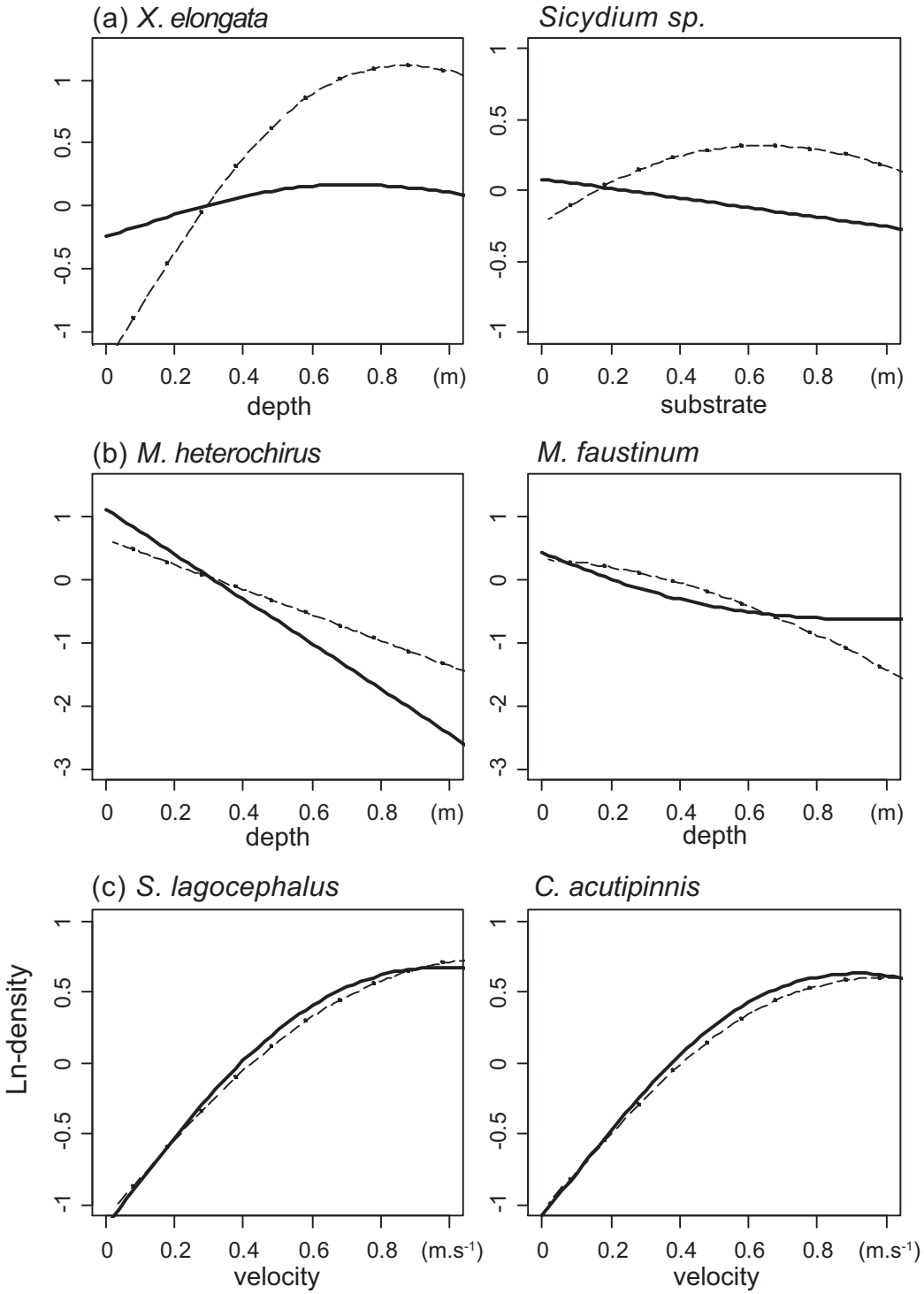
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