# Hydrological stability and otter trophic diversity: a scale-insensitive pattern?

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## ABSTRACT

Two recent works related otter (*Lutra lutra*, L., 1758) trophic patterns over large areas with the stability of aquatic ecosystems. Higher levels of instability lead to a reduced availability and/or predictability of fish, and consequently to a decrease of fish consumption by otters. The aim of the present study is to test these macrogeographical patterns in otter diet at regional and local-scale approaches. We analysed otter diet in Mediterranean streams in south-western Iberian Peninsula where clear hydrological stability gradients (related to drainage area or distance to the sea) could be defined. Hydrological stability was directly related to fish consumption and inversely to otter diet diversity in terms of occurrence and biomass, both at regional and local-scale approaches. The level of stability of aquatic ecosystems appears as a critical indirect factor modulating otter diet, through its effects on fish populations. The resulting trophic patterns are maintained from local to macrogeographical scales.

*Keywords:* trophic patterns, spatial scale, stability, carnivore ecology, Mediterranean streams, trophic ecology

*Running title:* Otter trophic patterns across scales

## INTRODUCTION

Ecological patterns and processes are sensitive to the scale of observation and, therefore, studies of the same phenomena conducted at different scales often yield different results (Wiens 2002). However, explanations for broad scale patterns, including possible emergent properties, often rely on mechanisms occurring at smaller scales (O'Neill et al. 1986; Brown et al. 2000). It is therefore important to investigate at this lower level to interpret patterns observed over a larger extent and relate phenomena across the scales (Levin 1992).

Regional, continental or even larger-scale approaches to describe patterns in the trophic ecology of different vertebrate predators are common in ecological literature (e.g. Herrera 1974; Iriarte et al. 1990; Korpimaki and Marti 1995; Goszczyński et al. 2000). The patterns observed in these works are usually related to biogeographic constraints or environmental gradients that are present in the large areas under examination. Hence, it is usually difficult or impossible to track the underlying mechanisms of these patterns at smaller scales, since local studies on trophic ecology are often performed in notably more homogeneous areas. Only particularly favourable circumstances can allow the study of predator food niche responses to small-scale gradients similar to those identified at broader scales.

The Eurasian otter (*Lutra lutra* L., 1758; simply otter hereafter) is a semi-aquatic predator specialized in obtaining virtually all its food in the water. Fish is usually the otter's main prey (Carss 1995) and is preferred over other types of prey whenever available (Erlinge 1968). Two recent literature reviews have related changes at different scales in the otter food niche breadth with the stability of the aquatic environments considered, after Lincoln et al. (1998), as the resistance to change (in this case, change in water levels following seasonal or meteorological circumstances) (Fig. 1A).

Jędrzejewska et al. (2001) showed a clear habitat-related gradient in otter's trophic diversity, going from the more stable sea shore, through lakes and rivers, to the more unstable small streams. Clavero et al. (2003) limited their analysis to European freshwater systems and compared trophic diversity in the relatively stable temperate habitats and in the highly variable Mediterranean ones. Both studies found a reduction in fish consumption and increased diet diversity with higher habitat instability, suggesting that aquatic habitat stability influences the availability of trophic resources for otters by affecting the abundance and predictability of fish populations (Fig. 1B).

The inverse relationship between hydrological stability and otter trophic diversity found by Jędrzejewska et al. (2001) and Clavero et al. (2003) could be investigated at smaller scales, by studying the trophic ecology of otters occupying environments with identifiable stability gradients. Fluvial ecosystems, and especially Mediterranean ones, offer a good opportunity to perform such tests. A strong and continuous flow stability gradient can be defined in Mediterranean watersheds from the relatively stable river mouths to upper stream stretches, which experience huge flow variations following the characteristic Mediterranean flow cycle (Gasith and Resh 1999; Magalhães et al. 2002a). Moreover, these longitudinal differences in stability in small Mediterranean catchments are related to fish abundance, which decreases in higher positions within catchments (Magalhães et al. 2002b).

Here, we use the results of otter diet analyses performed at two different spatial scales (regional and local) to test the trophic patterns previously detected at larger scales, which related aquatic habitat stability with otter's trophic diversity. If the indirect effect of habitat stability on otter diet diversity (through a direct effect on prey populations) observed in the macroscale analyses (Jędrzejewska et al.2001; Clavero et al. 2003) held true at smaller scales, fish contribution in otter diet would decrease, and diet diversity would increase as hydrological stability decreases towards upper stream sections.

## STUDY AREAS AND HYDROLOGICAL STABILITY GRADIENTS

### Regional scale: south-western Iberian basins

We collected otter spraints in 35 river and stream locations in SW Iberian Peninsula (Fig 2D). Collection was performed between April and June in 2001 and 2003. The whole area is characterised by a typical Mediterranean climate, with hot dry summers and cool humid winters (Blondel and Aronson 1999). The area is also quite homogeneous with regard to the topography, geology (mostly siliceous, with no calcareous elements) and hydrological regime. Sampling locations' altitude ranged from 35 to 543m above sea level (mean 259m). At least 20 spraints were collected at each location (range 21-94, mean 29.1), with a total of 1017 analysed spraints. None of the 35 locations had been used in previous review works on otter diet (i.e. Jędrzejewska et al.2001; Clavero et al. 2003).

We used drainage area at each sampling location as a measure of hydrological stability, since the characteristic flow fluctuations in Mediterranean fluvial ecosystems occur more intensively in small streams with reduced drainage areas (Gasith and Resh 1999; Magalhães et al. 2002b). Drainage areas ranged from 10 to 47800 km$^2$ (mean 3950 km$^2$). Area values were log (base 10) transformed prior to statistical analyses.

### Local scale: small coastal streams

The second study area comprises a narrow coastal band of about 150 square kilometres in S Spain, which runs from the El Valle River to the city of Algeciras, including mountain chains reaching over 800m above sea level. All water courses in the area are very small and dry-up during the summer months, due to the scarcity of precipitation recorded between June and September (Ibarra 1993). Details on the area's characteristics can be found in Clavero et al. (2004, 2005). Ten transects were chosen to include as much as possible of the variation in the gradient of habitat stability within the area. Thus, four transects were placed near the mouths of the four main streams and another four in their upper stretches. Two additional transects were located in the common estuary of two streams (La Jara and La Vega), and in the rocky coastal stretch to the east of the study area (Fig. 2D). Overall, 1682 spraints were analysed in the area, with a mean of 169.3 spraints analysed per transect (range 28-278), which were collected bimonthly between December 1999 and December 2001. A detailed description of otter diet composition in the area can be found in Clavero et al. (2004). Again, none of the data used at the local scales had been included in the reviews by Jędrzejewska et al. (2001) and Clavero et al. (2003).

Distance to the coast, measured following the river channel for each transect (in km), was used as an inverse surrogate of hydrological stability. In fact, marine and tidal-influenced ecosystems (minimum distance values) are the only ones in the area that maintain a constant water mass during the year, in contrast with upper stream sections (further from the coast), which only retain small isolated pools during summers (Clavero et al. 2005a). Distance to the coast was log (base 10) transformed prior to statistical analyses.

## ANALYTICAL METHODS

Spraint analysis followed standard procedures (Beja 1997). The analytical methodology is thoughtfully described in a previous work (Clavero et al. 2004). Diet composition was expressed as relative frequency of occurrence (RFO) (Mason and Macdonald 1986) and as proportion of biomass ingested by the otter. Original weights of otter prey were estimated through linear and non-linear regressions from key structure measurements and length-weight relationships (Clavero et al. 2004). Diet diversity was estimated using the Shannon-Wienner diversity index (H´), calculated from both RFO and percentage of biomass results. Six basic prey items (fish, crayfish and crabs, amphibians, reptiles, small aquatic arthropods and birds) were used for diet diversity calculation (mammal remains were never found in spraints), thus allowing appropriate comparisons with other diet studies (Jędrzejewska et al. 2001; Clavero et al. 2003). Thus, four otter diet descriptors were analysed: i) relative frequency of occurrence of fish; ii) diet diversity in terms of occurrence; iii) percentage of biomass ingested corresponding to fish; and iv) diet diversity in terms of biomass ingested.

The relationships between the hydrological stability gradients defined in each study area and otter diet descriptors were analysed through linear regression. Proportion data (frequency of occurrence and percentage biomass) were arcsine-transformed prior to statistical analyses.

## RESULTS

The hydrological stability gradients defined at regional and local scales were related to the four otter diet descriptors employed in this work. At the regional scale, the importance of fish in otter diet increased and otter diet diversity decreased as drainage area increased, both in terms of occurrence and biomass (Figure 3). In the small coastal streams, otter diet featured more fish in transects placed near or at the coast line, while diet diversity clearly increased in upper stream transects (Figure 4). Therefore, both at regional and local scales, higher hydrological stability is consistently related to an increase in fish consumption and a reduction of otter diet diversity.

# DISCUSSION

## Hydrological stability and otter diet

Stream order and stream size are surrogates of stream environmental stability (Matthews 1998). Therefore, although we have no direct quantitative measures of hydrological stability (e.g. variance of water levels), we assume that our definitions of stability gradients are appropriate surrogates of the hydrological stability of aquatic habitats in our study areas. Theoretical ecology predicts that animal populations (in this case, the otter fish prey) are more likely to reach abundances close to their carrying capacities in more stable environments (Townsend et al. 2003). In coastal and estuarine areas, as well as in large rivers, water volume is relatively constant and not limiting for fish compared to the highly fluctuant small inland streams, which consequently harbour a reduced richness and abundance of fish (Jędrzejewska et al. 2001; Magalhães et al. 2002a). It is a fact that other habitat features can change as we go up along the river continuum, with decreasing drainage areas and increasing altitudes (e.g. less buffered climatic conditions or reduced productivity). However, we believe that our study areas were homogeneous enough not to imply sharp climatic changes. At the regional scale, all studied locations featured similar climatic conditions, geological substrata were similar and maximum altitude was below 550m above sea level (e.g. well below the usual snow line in the southern Iberian Peninsula). At the local scale, all transects were less than 5 km from the sea and less than 150 m above sea level.

Mediterranean climatic characteristics reinforce the differences in stability along the river continuum gradient. Seasonal and interannual variations in the precipitation regime (Blondel  and Aronson 1999), particularly the strong summer drought, are the main factors structuring Mediterranean aquatic communities (Gasith and Resh 1999; Pires et al. 1999). Changes in the flow regime are extreme in small streams (Magalhães et al. 2002b; Morais et al. 2004), which are reduced to residual isolated pools during the summer (e.g. Prenda and Gallardo 1996; Clavero et al. 2005a).

We argue that hydrological instability leads to a broadening of otter diet niche through its negative effects on fish (i.e. otter's favourite prey) populations. An alternative interpretation of our results would be that otters' dietary patterns respond to a relative increase of alternative prey in more unstable habitats, that is, otters would behave as unselective foragers, consuming potential prey in relation to their availability in the field. It is however difficult to discern between these two explanations, since it might be unmanageable to make standardised and comparable measures of abundance of the different otter prey types (e.g. fish, crayfish, amphibians or insects) along a hydrological stability gradient. Nevertheless, captive otters have been shown to prefer fish when they are offered different prey types (Erlinge, 1968) and increases of the role of non-fish prey in otter diet have been related with periods of low fish availability (Kruuk, 1995). Moreover, the reduction in fish availability with increasing hydrological instability has been reported in Iberian Mediterranean basins (e.g. Magalhães et al. 2002b). Thus, it is likely that the enormous differences in hydrological stability in Mediterranean streams generate the clear spatial patterns observed in the otter feeding habits. Fish is the main prey of the otter in relatively stable aquatic habitats, but its importance decreases, and diet diversity increases, as ecosystem instability rises.

## Persistence of patterns across scales

Predators are usually forced to widen their trophic niches when their main prey becomes scarce or its availability is unpredictable (Erlinge 1986; Stephens and Krebs 1986). Thus, different studies have reported otter diets that included important proportions of non-fish prey (e.g. Adrián and Delibes 1987; Brzeziński et al. 1993; Beja 1996; Sulkava 1996). Both Jędrzejewska et al. (2001) and Clavero et al. (2003) have related this reduced predation upon fish to habitat or biogeographical constraints derived from instability in aquatic ecosystems, which makes fish populations scarce or unpredictable.

We have shown that the relationship between habitat stability and the breadth of the otter trophic niche also exists at regional and local (i.e. population) scales. This means that the scaling domain (sensu Wiens 1989) of the inverse relationship between otter trophic diversity and hydrological stability of the aquatic environments is large enough to include from the local population to the biome. Consistent patterns of foraging behaviour or trophic resource tracking across different spatial scales have been previously described regarding marine predators (Benoit-Bird and Au 2003), terrestrial predators (Ives et al. 1993) and terrestrial herbivores (Schaefer and Messier 1995). However, to our knowledge, there are no previous works showing consistent patterns in predator's diet composition across a wide range of spatial scales.

The consistency of the patterns observed at different scales strongly suggests that the mechanisms used to explain them at the population level are also applicable to the comparisons between different ecosystems (rivers, lakes, sea shores; Jędrzejewska et al. 2001) or between the same ecosystems in different bioclimatic regions (Temperate *versus* Mediterranean rivers; Clavero et al. 2003). Moreover, due to the reduced size of our local scale study area (see Figure 2D), it could be argued that individual feeding behaviour can lay at the base of the trophic patterns described at different scales, since the same individual otter could easily predate in the highest and lowest transects in our area. The use of least stable (i.e. less suitable) transects by otters at the local scale could then be related to intraspecific competition (Fretwell and Lucas 1969), being enhanced by the saturation of most suitable habitats. However, other factors, such as human perturbation (e.g. Clavero et al. 2006) or the exploitation of temporally abundant resources (e.g. breeding amphibians) (Weber 1990; Clavero et al. 2005b), could also favour the use of these unstable areas.

We have stated that working at different scales frequently leads to different or even contradictory explanations of natural phenomena (Wiens et al. 1993). For instance, Neilson and Wullstein (1983) showed an opposite relationship between oak seedling mortality and precipitation at local and regional scales. However, on some occasions, the persistence of patterns across scales has been emphasized. Brown et al. (2000) found that the structure of desert rodent communities, at scales ranging from local to continental, could be largely explained by interspecific competition. In a similar way, our study indicates that the same pattern in otter trophic ecology can be described at different scales, suggesting that the stability of aquatic ecosystems is a main factor influencing the breadth of the otter trophic niche, through its direct effects on the abundance and predictability of fish populations.

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## Figure captions

**Figure 1.** A) variation in the relative frequency of (RFO) occurrence of fish and otter diet diversity (mean ± SD) in different aquatic ecosystems (sea, lakes and rivers) in the Palaearctic (after Jędrzejewska et al. 2001) and in freshwater ecosystems in different European climatic areas (temperate and Mediterranean) (after Clavero et al. 2003); and B) suggested variation in otter trophic diversity and fish communities characteristics in relation to hydrological stability (after Clavero et al. 2003).

**Figure 2.** Location of the different study areas considered in this work: A) diet studies revised by Jędrzejewska et al. (2001) throughout the Palaearctic; B) diet studies revised by Clavero et al. (2003) in European freshwater habitats; C) 35 sampling locations in river basins in south-western Iberian Peninsula; and D) 10 transects in small coastal streams in the south of the Iberian Peninsula. Quadrates in maps A, B and C represent areas enlarged in maps B, C and D, respectively.

**Figure 3.** Relationships between the hydrological stability gradient at regional scale (i.e. drainage area) and RFO of fish, proportion of fish biomass, RFO diversity and biomass diversity of otter diet in 35 study locations in south-western Iberian Peninsula.

**Figure 4.** Relationships between the hydrological stability gradient at local scale (i.e. distance from the sea) and RFO of fish, proportion of fish biomass, RFO diversity and biomass diversity of otter diet in 10 study transects in small coastal streams in south Iberian Peninsula.

FIGURE 1

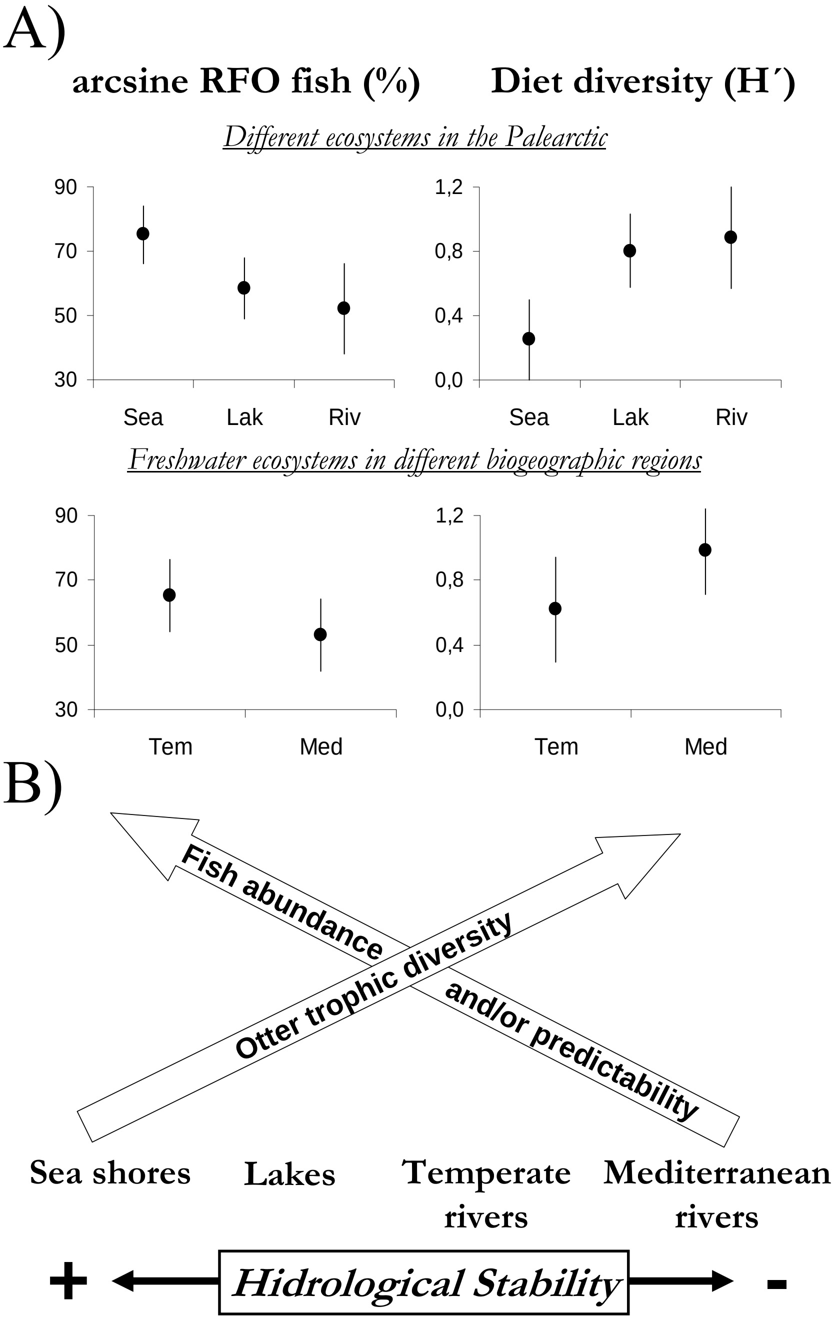

A)
arcsine RFO fish (%)
Diet diversity (H´)
Different ecosystems in the Palearctic
90
70
50
30
Sea
Lak
Riv
1,2
0,8
0,4
0,0
Sea
Lak
Riv
Freshwater ecosystems in different biogeographic regions
90
70
50
30
Tem
Med
1,2
0,8
0,4
0,0
Tem
Med
B)
Fish abundance
and/or predictability
Otter trophic diversity
Sea shores
Lakes
Temperate rivers
Mediterranean rivers
+
Hidrological Stability
-

FIGURE 2

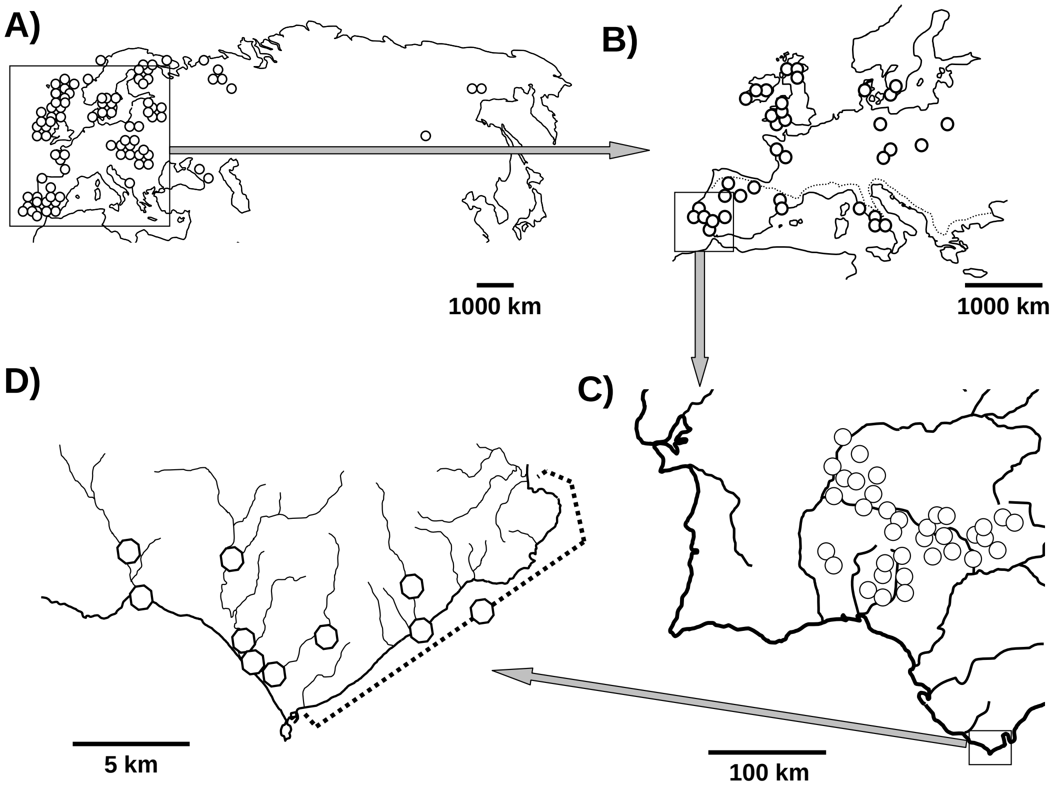
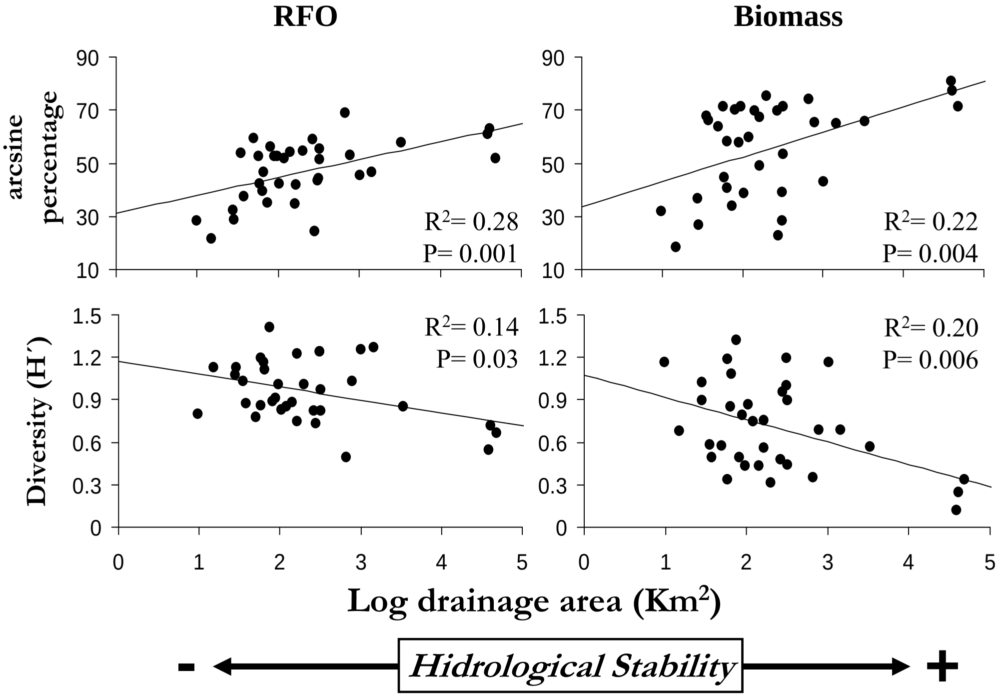
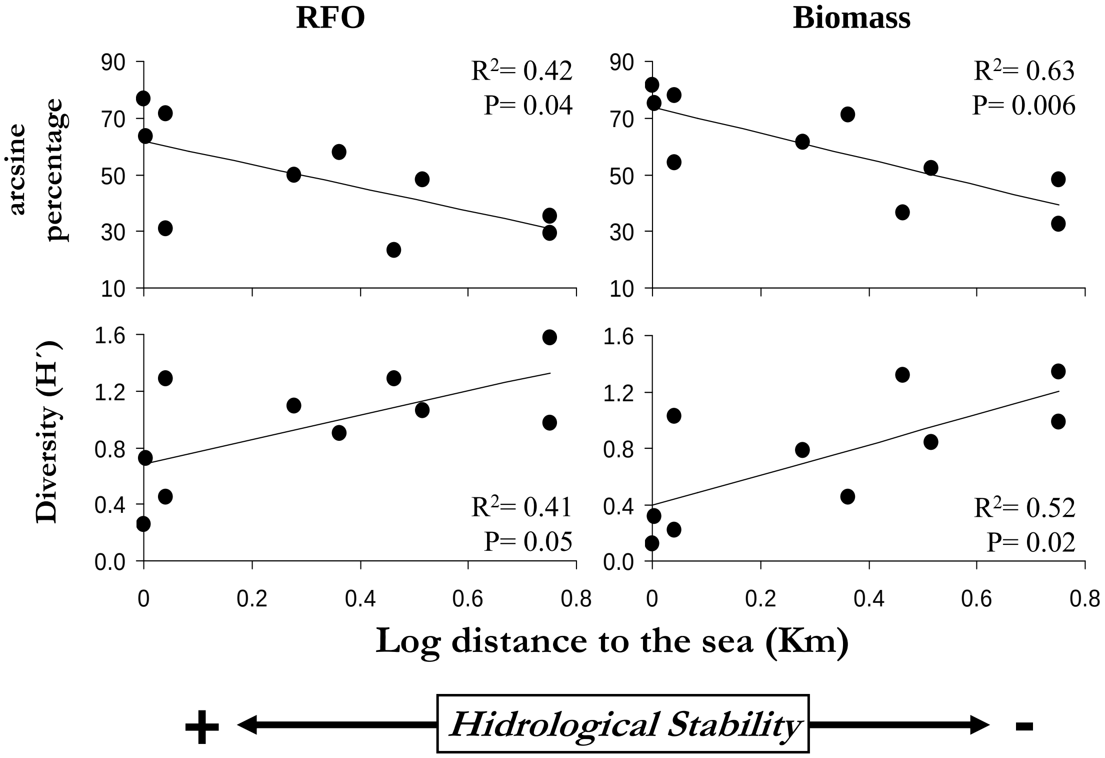


FIGURE 3


RFO
Biomass
arcsine percentage
Diversity (H´)
90
70
50
30
10
1.5
1.2
0.9
0.6
0.3
0
R2= 0.28
P= 0.001
R2= 0.22
P= 0.004
R2= 0.14
P= 0.03
R2= 0.20
P= 0.006
0
1
2
3
4
5
Log drainage area (Km2)
-
Hidrological Stability
+

10

FIGURE 4


RFO
Biomass
arcsine percentage
Diversity (H´)
R²= 0.42
P= 0.04
R²= 0.63
P= 0.006
R²= 0.41
P= 0.05
R²= 0.52
P= 0.02
90
70
50
30
10
1.6
1.2
0.8
0.4
0.0
0
0.2
0.4
0.6
0.8
Log distance to the sea (Km)
+
Hidrological Stability
-