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Structure and functioning of intertidal food webs along an avian flyway: a comparative approach using stable isotopes

Teresa Catry^{*1}, Pedro M. Lourenço¹, Ricardo J. Lopes², Camilo Carneiro³, José A. Alves^{4,5}, Joana Costa⁶, Hamid Rguibi-Idrissi⁷, Stuart Bearhop⁸, Theunis Piersma^{9,10} and José P. Granadeiro¹¹

¹Centro de Estudos do Ambiente e do Mar, Museu Nacional de História Natural e da Ciência, Universidade de Lisboa, Rua da Escola Politécnica 58, 1250-102 Lisboa, Portugal; ²CIBIO, Centro de Investigação em Biodiversidade e Recursos Genéticos, InBIO Laboratório Associado, Universidade do Porto, 4485-661 Vairão, Portugal; ³Museu Nacional de História Natural e da Ciência, Universidade de Lisboa, Rua da Escola Politécnica 58, 1250-102 Lisboa, Portugal; ⁴Centro de Estudos do Ambiente e do Mar, Universidade de Aveiro, Campus Universitário de Santiago, 3180-193 Aveiro, Portugal; ⁵South Iceland research Centre, University of Iceland, Tryggvagata 36, IS-800 Selfoss Iceland; ⁶Departamento de Biologia Animal Faculdade de Ciências da Universidade de Lisboa, 1749-016 Lisboa, Portugal; ⁷Faculté des Sciences, Equipe de Recherche: Valorisation des Ressources Naturelles et Biodiversité, Université Chouaib Doukkali, El Jadida, 24000 Morocco; ⁸Centre for Ecology & Conservation University of Exeter, Penryn Campus, Penryn, Cornwall TR10 9EZ, UK; ⁹NIOZ Royal Netherlands Institute for Sea Research, PO Box 59, 1790 AB Den Burg, Texel, The Netherlands; ¹⁰Animal Ecology Group, Centre for Ecological and Evolutionary Studies, University of Groningen, PO Box 11103, 9700 CC Groningen, The Netherlands; and ¹¹Departamento de Biologia Animal, Centro de Estudos do Ambiente e do Mar, Faculdade de Ciências da Universidade de Lisboa, 1749-016 Lisboa, Portugal

Summary

1. Food webs and trophic dynamics of coastal systems have been the focus of intense research throughout the world, as they prove to be critical in understanding ecosystem processes and functions. However, very few studies have undertaken a quantitative comparison of entire food webs from a key consumer perspective across a broad geographical area, limiting relevant comparisons among systems with distinct biotic and abiotic components.

2. We investigate the structure and functioning of food webs in four tidal ecosystems of international importance for migratory shorebirds along the East Atlantic Flyway: Tejo estuary in Portugal, Sidi Moussa in Morocco, Banc d'Arguin in Mauritania and Bijagós archipelago in Guinea-Bissau. Basal food sources, shorebirds and their prey (benthic invertebrates) were sampled in all areas, and Bayesian stable isotope mixing models and community-wide metrics were used in a comparative analysis among areas.

3. Significant differences among study areas were found in the structure of food webs, as well as in the relative importance of basal resource pools supporting each food web. Overall, the food web of Banc d'Arguin was characterized by lower trophic diversity and higher functional redundancy than the other sites. This result might be explained by the low number of trophic pathways of organic matter transfer in this seagrass-dominated system which, as a fossil estuary, lacks inputs from both freshwater and nutrient-rich offshore oceanic waters.

4. Structure of shorebird communities was consistent with the main organizational patterns found for each food web, highlighting the less diverse character of the community of Banc d'Arguin. At Banc d'Arguin and Bijagós archipelago, which displayed the smallest and largest isotopic niche widths in bird assemblage, respectively, mean niche overlap among species was low, suggesting high interspecific partitioning in resource use. Tropical systems typically offer

*Correspondence author. E-mail: teresa.catry@gmail.com
TC and JPG contributed equally to this study.

comparatively lower harvestable prey biomass for shorebirds and might thus strengthen inter-specific competition, leading to low niche overlap among species.

5. Our study reveals relevant differences in the structure of food webs and shorebird communities in coastal areas along an avian flyway. While differences in trophic redundancy of food webs point to distinct levels of ecosystem resilience, contrasts in the organization of shorebird communities highlight the plasticity in the foraging behaviour of species inhabiting areas with distinct environmental conditions.

Key-words: Bayesian mixing models and community metrics, coastal tidal ecosystems, migratory shorebirds, trophic structure

Introduction

Large coastal tidal areas, such as estuaries, lagoons and shallow oceanic waters, are among the most productive ecosystems on Earth. Due to their high productivity, coastal sites world-wide harbour large numbers of waterbirds which use them in seasonal succession as they migrate along flyways (Delany *et al.* 2009). Avian migrants interact with the resident fauna and thus influence the trophic networks at multiple sites (Bauer & Hoyle 2014). The East Atlantic Flyway is a migration route used by millions of shorebirds, connecting high-latitude breeding grounds to wintering areas located along the western coasts of Europe and Africa (Delany *et al.* 2009). This flyway encompasses an intercontinental network of extremely diverse coastal wetlands (e.g. marshes, mangroves or seagrass-dominated habitats) at temperate, subtropical and tropical latitudes, most of which are internationally recognized for their ecological and economic importance (Delany *et al.* 2009). These areas sustain large populations of migratory shorebirds that, during low tide, feed on massive stocks of macroinvertebrates on intertidal flats. Shorebirds have been shown to exert top-down regulation on prey populations via direct predation or trophic cascades, as well as to impact ecosystem processes, such as nutrient cycles (van Gils *et al.* 2012; Ahmedou Salem *et al.* 2014). Likewise, several aspects of the migratory ecology of shorebirds (e.g. fuelling rates of pre-migratory birds) are strongly influenced by the prevailing ecological processes (e.g. diversity, quality and biomass of invertebrate prey) which may differ markedly among different sectors of their flyway (Piersma *et al.* 2005).

Coastal habitats are increasingly threatened by human activities impacting processes such as primary production and nutrient cycling, but also depressing emblematic predator populations and their prey (Lotze *et al.* 2006). Therefore, building a thorough understanding of food webs in these systems over a large geographic scale can allow us to identify the effects of global changes on these critical habitats. This is particularly timely and relevant for many wetlands in Africa which are poorly known and currently imperilled by rapidly increasing human pressures (Junk 2002).

The challenge to decipher the structure and functioning of marine/estuarine ecosystems has received a boost with

the generalization of stable isotope analysis (SIA) during the last few decades. Stable isotope signatures of carbon ($\delta^{13}\text{C}$) and nitrogen ($\delta^{15}\text{N}$) found in the biological components of a system can be used to trace element cycles and their incorporation in food webs, measure several dimensions of ecological niches of consumers and develop models of trophic structure (e.g. Bouillon, Connolly & Gillikin 2011; Layman *et al.* 2012). Recently, a set of community metrics based on stable isotopes have been successfully used for characterizing food webs (Layman *et al.* 2007; Abrantes, Barnett & Bouillon 2014). Concurrently, new statistical developments have enabled quantitative comparisons of food webs across environmental gradients, or of the same food webs over a given time window (Jackson *et al.* 2011). Quantifying isotopic niche width of individuals has also become a generalized proxy for assessing trophic ecology of consumers (e.g. Quevedo, Svanbäck & Eklöv 2009; Bocher *et al.* 2014).

In this study, we undertake a quantitative comparison of the structure and functioning of food webs in four tidal systems across the East Atlantic Flyway by including all relevant links leading to shorebirds. We selected four internationally important areas for shorebirds: Tejo estuary (Portugal), Sidi Moussa (Morocco), Banc d'Arguin (Mauritania) and Bijagós archipelago (Guinea-Bissau). More specifically, our objectives include the following: (i) a comparison of the major basal food sources and nutrient pathways fuelling secondary production among the four study ecosystems, (ii) a quantitative description of the trophic structure and diversity of tidal environments using community metrics derived from stable isotopic data, (iii) interpreting and comparing trophic structure among and within shorebird communities and (iv) assessing trophic resources partitioning within shorebird communities and comparing ecological overlap among communities of all study areas.

Our predictions are that contrasting environmental conditions, in particular, influence of marine and freshwater inputs, anthropogenic pressure and dominance of primary producers, will drive relevant differences in the functioning of study systems, namely in the number and type of sources fuelling food webs. Differences in structure are also to be expected, and we anticipate that systems showing a higher number of fuelling sources will present a more

complex trophic structure and lower overall trophic redundancy (i.e. lower proportion of trophically equivalent taxa). Regarding shorebird communities, we predict that in tropical systems, which typically show a lower ratio between stock size of macrobenthic fauna and shorebird density, the constraining effects of interspecific competition might lead to reduced isotopic niches at the species level, and low niche overlap among species (Bolnick *et al.* 2010).

Materials and methods

STUDY AREAS

This study took place in four key wintering areas for shorebirds within the East Atlantic Flyway (Delany *et al.* 2009). Tejo estuary, the northernmost studied site (Portugal; 38°45'N, 09°01'W), comprises an intertidal area of 97 km², mostly composed of mudflats. Saltpans and saltmarshes, dominated by *Spartina maritima*, *Halimione portulacoides* and *Sarcocornia fruticosa*, are available as feeding but mostly roosting habitats for shorebirds.

Sidi Moussa is a coastal lagoon situated on the Moroccan Atlantic coast (32°58'N, 8°45'W), with an area of 4.2 km² and with a permanent connection to the ocean, thus exposed to a tidal regime. The intertidal areas are composed of mud and sandflats, partly covered by the seagrass *Zostera noltii*. Vegetation in the margins of the main lagoon channels includes *S. maritima* and *Sarcocornia perennis*. Saltpans and an important agricultural area border the lagoon.

The Banc d'Arguin, in Mauritania (19°52'N, 16°17'W), is an area of tidal flats and shallow inshore waters in the tropical Saharan coast, occupying more than 500 km², covered by extensive beds of the seagrasses *Z. noltii* and lower down *Cymodocea* sp. Sampling sites were located near the village of Iwik, at Baie d'Aouatif and Ebelk Aiznay.

The Bijagós archipelago is located off the coast of Guinea-Bissau (11°12'N, 15°53'W) and comprises 88 islands and islets. The intertidal area comprises around 760 km² of mud and sandflats, 350 km² of which are covered by mangroves (including *Rizophora* sp., *Laguncularia* sp., *Avicennia* sp. and *Conocarpus erectus*). All sampling took place in the islands of Bubaque, Canhabaque and João Vieira.

SAMPLE COLLECTION AND PROCESSING

Samples of water for particulate organic matter (POM) analysis, sediment for organic matter (SOM) analysis, benthic microalgae, zooplankton and dominant species of macroalgae, plants, macroinvertebrates and shorebirds (toenails) were collected in the winters of 2012–2013 and 2013–2014 in all study areas except in the Bijagós, where sampling took place only in 2013–2014 (see Tables S1 and S2 in Supporting Information).

Whenever possible, at least three replicates were collected for each material component of the system, except for water, sediment, zooplankton and microalgae, for which between 1 and 2 samples were taken (Table S1). Detailed methodological protocols of sample collection and processing are presented in Appendix S1.

Macroinvertebrate sampling was directed towards potential shorebirds' prey taxa and size classes. At Tejo estuary and Sidi Moussa, where more information on shorebird diet was already available (e.g. Kersten *et al.* 1981; Moreira 1994; Lourenço *et al.* 2008; Catry *et al.* 2012a), sampling of macroinvertebrates was less extensive than at the remaining areas.

Sampling of toenails of shorebirds took place mainly between late December and February, to ensure that isotopic signatures of toenails were exclusively representing their local wintering diet

(assuming that birds have been in their wintering grounds since early November: Lourenço *et al.* (2015) indicate half-lives of 27 and 35 days for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in toenails of captive dunlins; see also Bearhop *et al.* 2003).

STABLE ISOTOPE ANALYSIS

All samples (except bird toenails) were ground into a homogeneous powder using mortar and pestle. Lipid extraction was performed in macroinvertebrate samples following Logan *et al.* (2008; Appendix S1). Samples of sediment, zooplankton, bivalves, gastropods and crustaceans were tested for the presence of carbonates and acidified following Vinagre *et al.* (2008) whenever the test was positive (Appendix S1). A non-acidified subsample was always kept for separate nitrogen isotope analysis. Toenails of shorebirds were prepared as described in Catry, Martins & Granaideiro (2012b; Appendix S1).

Between 0.5 mg and 1.0 mg of each replicate from all components were stored in tin cups for stable carbon and nitrogen isotope assays. Isotopic ratios were determined by continuous-flow isotope-ratio mass spectrometry (CF-IRMS). Results are presented conventionally as δ values in parts per thousand (‰) relative to the Vienna Pee Dee Belemnite (VPDB) for $\delta^{13}\text{C}$, and atmospheric nitrogen (N_2) for $\delta^{15}\text{N}$.

DATA ANALYSIS

Contribution of basal food sources to macroinvertebrate consumers

To compare the relative importance of fuelling basal food sources to secondary production among the four study ecosystems, dual-isotope mixing models were used to estimate the contribution of carbon and nitrogen food sources (POM, SOM and primary producers) to the different benthic macroinvertebrates, according to taxa and functional group. Macroinvertebrates were thus grouped by taxa (class) and further classified into feeding guilds according to published literature (Fauchald & Jumars 1979; Macdonald *et al.* 2010) and our own data. We used SIAR package running in R (Parnell *et al.* 2008) to produce all mixing models, and we ran separate models for species showing very distinct isotopic signatures from their group. Isotopic data from all C₃ plants were pooled to improve the quality of isotopic estimates by reducing the number of potential sources and increasing discriminant power of the models (Phillips *et al.* 2014). Trophic discrimination factors of 3.4 ± 1.0 for $\delta^{15}\text{N}$ and 0.4 ± 1.3 for $\delta^{13}\text{C}$ were used in the models, following Post (2002). Recent studies suggested that mixing models may be sensitive to variation in discrimination factors (Bond & Diamond 2011). Thus, we conducted a sensitivity analysis by re-running all our models and calculating the median contribution of each source using all combinations of trophic discrimination values lying within the means used in our initial model \pm 1SD (−0.9–1.7 and 2.4–4.4 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively), while still including the original standard variation. Unlike Bond & Diamond (2011), we found that in most situations, even a substantial variation in trophic discrimination factors did not generate much variation in the contribution of food source estimated by SIAR models and therefore, our main findings remained unchanged (Fig. S1).

Community and population iso-space metrics

Carbon and nitrogen isotopic signatures of consumers, that is macroinvertebrates (grouped by taxa and feeding guild) and shorebirds (as unique groups), were used to investigate the structure of trophic webs in each study area using the community-wide metrics proposed by Layman *et al.* (2007; hereafter Layman's

metrics). Lucinidae bivalves were not included in these analyses as they show a very distinct metabolism, characterized by an endosymbiotic relationship with sulphide-oxidizing bacteria (van der Heide *et al.* 2012). Chironomidae larvae were also excluded as they were only sampled in two of the study areas and have no taxonomic/guild equivalent in the other areas. To estimate iso-space metrics of shorebird communities in each study area, individuals were pooled according to species.

Three Layman's community metrics reflect trophic diversity derived from $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ bi-plots. $\delta^{15}\text{N}$ range (NR) and $\delta^{13}\text{C}$ range (CR) provide information on the trophic length and niche diversification of basal resources, respectively. Mean distance to centroid (CD), measured as the average Euclidean distance of each consumer's group to the $\delta^{13}\text{C}$ - $\delta^{15}\text{N}$ centroid, gives a measure of the average degree of trophic diversity. The two other Layman's metrics, mean nearest neighbour distance (MNND) and standard deviation of nearest neighbour distance (SDNND), represent measures of trophic redundancy. MNND provides information on overall density of community members packing, that is the proximity of species within the isotopic space. Low values of MNND indicate a large proportion of members with similar trophic preferences. SDNND is a measure of evenness of community components packing, with low values representing a more uniform distribution of trophic niches (Layman *et al.* 2007).

Sampling error in the mean values of isotope ratios of community members delivers uncertainty to all Layman's metrics, and therefore, we used a Bayesian approach to estimate these community metrics using SIAR package in R (Parnell *et al.* 2008; Jackson *et al.* 2011; R Core Team 2013). This Bayesian technique also allows for statistical comparisons among communities based on uncertainty measures around metrics' estimates. Jackson *et al.* (2011) also proposed the use of areas of standard ellipses, which contain ca. 40% of all data, to measure and compare isotopic niche width among communities or populations, since this estimate is less sensitive to extreme values and low sample size than total area. We calculated Bayesian standard ellipse areas (SEA_B) and small sample size-corrected standard ellipse areas (SEA_C), for the studied communities and populations. SEA_B are not affected by bias associated with the number of community members, therefore allowing comparisons among communities regardless of the number of components (Jackson *et al.* 2011).

To compare the trophic structure of communities among sites showing substantial variation in isotope ratios of basal resources, an isotopic baseline correction is required (e.g. Olsson *et al.* 2009). Thus, we have standardized all $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values of consumers by subtracting the mean value of site-specific basal sources (contributing with more than 10% for at least one guild of consumers) and dividing by the range value of the same sources.

Overlap in SEA_C among shorebird populations was used as a measure of isotopic niche partitioning within communities. Isotopic niche overlap was calculated for all pairs of species. For each species (*i*) in one pair (*i,j*), a value of overlap ($\text{Ov}_{[ij]}$) was calculated as the ratio between the area of overlap between the two SEA_C ($A_{[i,j]}$) and its own SEA_C ($A_{[i]}$), expressed as a proportion ($\text{Ov}_{[ij]} = A_{[i,j]}/A_{[i]}$). Average overlap per species was estimated afterwards, as the average of all overlaps involving that species.

Results

CONTRIBUTION OF BASAL FOOD SOURCES TO MACROINVERTEBRATE CONSUMERS

The $\delta^{13}\text{C}$ signatures of basal food sources (POM, SOM and primary producers) showed a wide range of values in the four study areas (Fig. 1). In the Tejo estuary, C_4 vegetation (saltmarsh *S. maritima*) contributed the most to the

food web, although C_3 plants and the macroalgae *Ulva* sp. also had non-negligible contributions for some groups (Fig. 2). At Banc d'Arguin, seagrass was clearly the dominant source for most functional groups; only for filter-feeding bivalves, the models suggest a shared dominance of seagrass with microalgae and SOM. At neither Sidi Moussa nor Bijagós archipelago was there evidence for a dominant contributor among the sampled food sources, although SOM seemed to be a relevant source for bivalves and polychaetes in Bijagós (Fig. 2).

STRUCTURE OF FOOD WEBS

Despite some overlap recorded among macroinvertebrates belonging to different taxa and/or functional groups, in all study areas, either polychaetes or crustaceans combining detritivory and predatory strategies occupied the higher trophic positions of the food web (higher $\delta^{15}\text{N}$ values, Fig. 1). Also, with few exceptions, filter feeders (bivalves) had an intermediate trophic position. Regarding $\delta^{13}\text{C}$ ratios, primary consumers displayed a generally high overlap, with the exception of filter-feeding bivalves of Banc d'Arguin. Although generally within the higher trophic levels of food webs, shorebirds were close to that of their potential prey within the isotopic space (Fig. 1).

We found several differences in the trophic structure of the communities of consumers among study areas (Fig. 3, Table S3). Overall, the food web of Banc d'Arguin presented the most distinctive structure, characterized by shorter chain length (lower NR), lower trophic diversity (lower CD) and higher trophic redundancy (lower MNND and SDMNND; all comparisons $\geq 90\%$, except SDMNND Banc d'Arguin vs. Bijagós; Table S3). Moreover, the areas of the SEA_B estimated for Banc d'Arguin were also smaller than those from any of the remaining study areas (all comparisons $\geq 85\%$, Fig. 3, Table S3). Sidi Moussa community had the smallest CR (all comparisons $\geq 90\%$, Table S3).

TROPHIC STRUCTURE AND NICHE COMPARISONS AMONG AND WITHIN SHOREBIRD COMMUNITIES

Shorebird communities showed considerable differences in their trophic structure among study sites (Fig. 4). The most contrasting differences, both when analysing the whole communities or when considering only species common to the four study areas, were recorded between Banc d'Arguin and Bijagós. As observed for the consumers' food webs, the shorebird community of Banc d'Arguin showed the lowest NR, CD, MNND and SDMNND (probabilities of all comparisons $\geq 80\%$; Table S4), while the Bijagós community generally presented the highest values. The horizontal structure of the shorebird community of Tejo estuary, given by CR, was overall wider than the remaining ones (Fig. 4, Table S4). Differences in the areas of Bayesian ellipses (SEA_B) followed the previous pattern, with Banc d'Arguin and Bijagós showing the smallest and the largest isotopic niches, respectively (Fig. 4, Table S4).

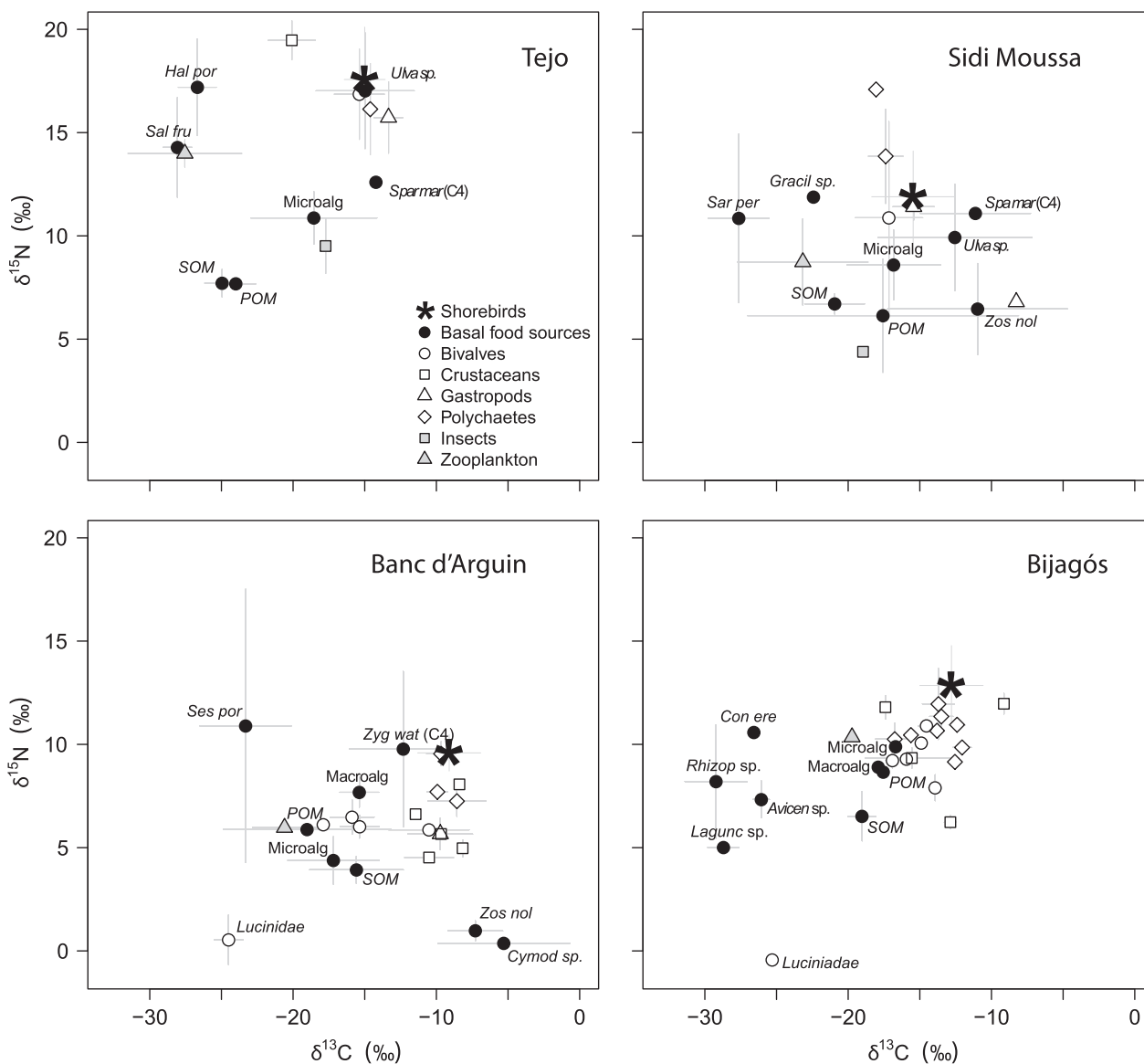


Fig. 1. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures (mean \pm SD) of basal food sources (POM, SOM and producers) and consumers in Tejo estuary, Sidi Moussa, Banc d'Arguin and Bijagós archipelago. Basal food sources: POM = (suspended) particulate organic matter; SOM = sediment organic matter; C3 producers: Hal por = *Halimione portulacoides*, Sar fru = *Sarcocornia fruticosa*, Sar per = *Sarcocornia perennis*, Ses por = *Sesuvium portulacastrum*, Rhi = *Rhizophora* sp., Con ere = *Conocarpus erectus*, Lag = *Laguncularia* sp., Avic = *Avicennia* sp.; C4 producers: Spa mar = *Spartina maritima*, Zyg wat = *Zygophyllum waterlotii*; Algae: Macroalg = macroalgae, Microalg = microalgae, Gracil sp. = *Gracillaria* sp.; Seagrasses: Zos nol = *Zostera noltii*, Cym sp. = *Cymodocea* sp.

The mean overlap in isotopic niches (SEA_C ellipses) among shorebird species was higher at the Tejo estuary and Sidi Moussa as compared with Banc d'Arguin and Bijagós (one-way ANOVA, $F_{3, 36} = 2.85$, $P = 0.014$; Fig. 5). Overall, red knots and bar-tailed godwits exhibited the lowest levels of niche overlap within local communities (Fig. 5).

Discussion

Very few studies have quantitatively compared the 'topography' of food webs under different environmental

conditions (but see e.g. França *et al.* 2011; Olin *et al.* 2013), and only one has adopted a large-scale community-based comparative approach from the perspective of a key predator (Abrantes, Barnett & Bouillon 2014). In the present study, community-wide metrics based on stable isotopes revealed considerable differences in the structure of food webs leading to shorebirds in four tidal systems of Europe and West Africa, which might be partly driven by differences in the relative importance of basal resource pools supporting food webs. Moreover, shorebird communities also showed distinct trophic structures and different degrees of resource partitioning among areas.

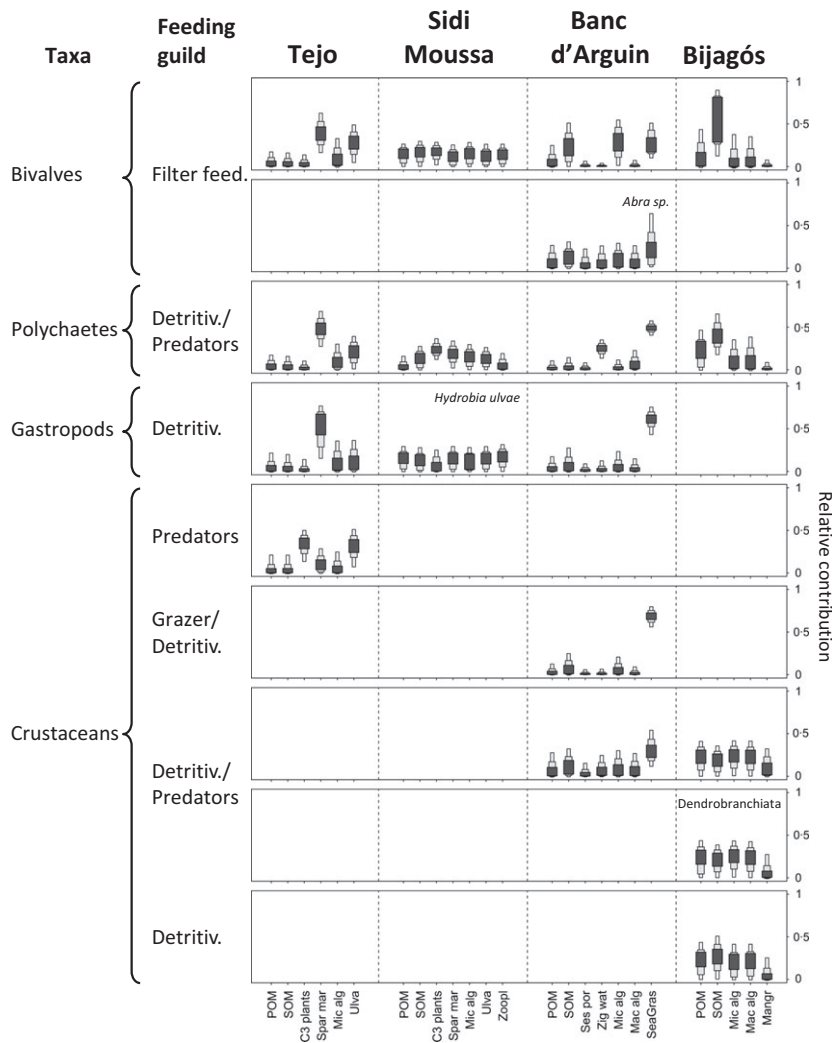


Fig. 2. Relative contribution of basal food sources to the diet of macroinvertebrates in the four study areas as estimated by mixing models. In each study area, contributions were estimated for taxa-specific feeding guilds. For taxa showing distinctive isotopic signatures, contributions were estimated and represented separately. Empty slots occur whenever a particular taxa and/or feeding guild was not sampled in one study area. Taxa included in each feeding guild are presented in Table S1.

STRUCTURE AND DYNAMICS OF FOOD WEBS

The food web structure of Banc d'Arguin was the most distinctive among the studied systems. In fact, NR, CD, MNND and SDMNND were generally lower at Banc d'Arguin than in other areas, suggesting a simpler trophic structure, with a large proportion of members characterized by similar trophic profiles, that is, likely playing similar functional roles (higher trophic redundancy). The main sources fuelling the benthic secondary production of Banc d'Arguin have been long discussed, because the system has been considered isolated from the influence of the upwelling off the coast of Mauritania and believed to be nutrient-limited (Honkoop *et al.* 2008; Clavier *et al.* 2014). As described in other seagrass-dominated systems (e.g. Lebreton *et al.* 2011; Vafeiadou *et al.* 2013), our results suggest that seagrass and to a lesser extent microalgae (mainly for suspension feeding bivalves) are the major source of organic matter for consumers at Banc d'Arguin. Given the isolation of the intertidal flats from the nutrient-rich offshore oceanic waters and the lack of freshwater inputs, the low number of trophic pathways of organic matter transfer might explain

the high trophic redundancy recorded within the food web in this area.

Results from SIAR mixing models revealed that the main basal food sources supporting secondary production differ among sites. As previously shown for the Tejo estuary (Vinagre *et al.* 2008), C_4 *S. maritima* saltmarshes have a high contribution to the food web, but both macro- and microalgae, and also C_3 halophytes, seem to have non-negligible contributions for particular consumers. In Sidi Moussa, both the model results and the $\delta^{13}C$ - $\delta^{15}N$ bi-plot suggest a variety of sources and trophic pathways, but different trophic guilds likely rely upon the same basal food sources (as reflected by the smallest CR value). A food web supported by several sources seems to be also the case in Bijagós. However, isotopic signatures of macroinvertebrates from the Bijagós are not clearly within the iso-space encompassed by their potential food sources (being mostly $\delta^{13}C$ -enriched even when correcting for trophic discrimination factor, Fig. 1), suggesting that non-sampled sources (e.g. different macroalgae species, epiphytes) might be contributing to the overall food web, or that sampling should have been more extensive to avoid

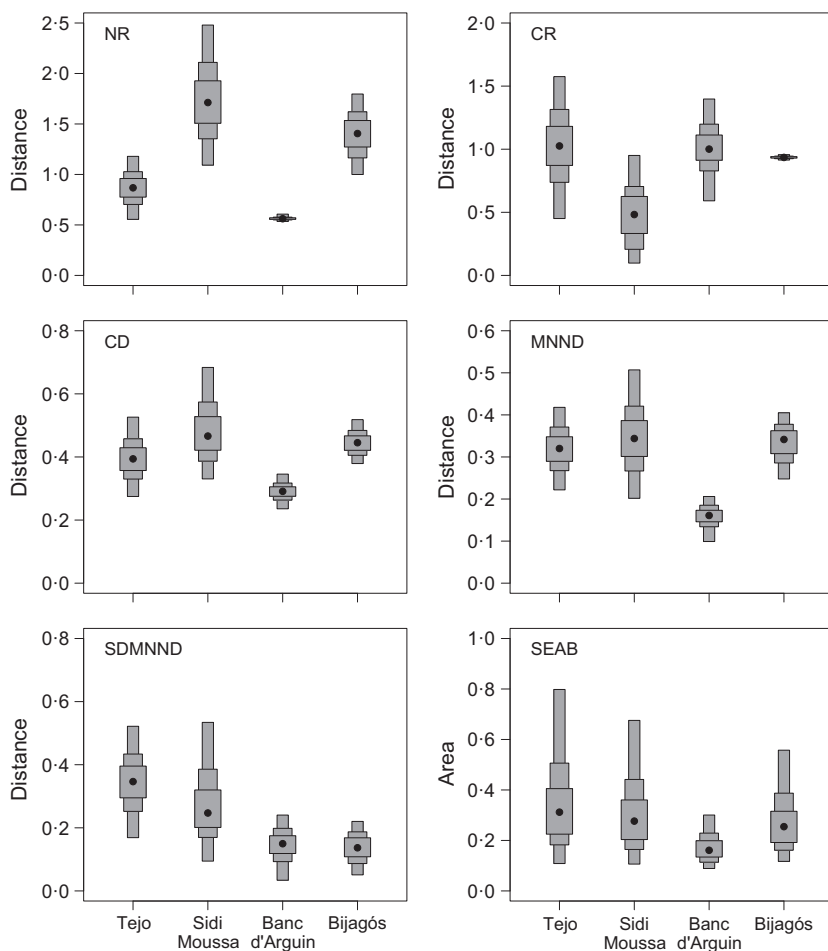


Fig. 3. Bayesian results of the Layman's community-wide metrics and standard Bayesian ellipse area (SEA_B) for the communities of consumers in the four study areas. Black dots represent the mode, and boxes present the 50%, 75% and 95% credible intervals. NR = $\delta^{15}N$ range, CR = $\delta^{13}C$ range, CD = mean distance to centroid, MNND = mean nearest neighbour distance, SDMNND = standard deviation of mean nearest neighbour distance.

potential local heterogeneities. Although mangroves can attain high levels of primary production, their potential role as a major source of nutrients to primary consumers remains in discussion (Bouillon, Connolly & Gillikin 2011). At Bijagós, mangroves seem to play a secondary role as a basal food source for the trophic web.

Shorebirds, as secondary consumers, were surprisingly close to their potential prey in the isotopic space, hardly suggesting roles as top consumers within the studied food webs. Indeed, the expected enrichment of 3–4 ‰ for $\delta^{15}N$ (Post 2002; Lourenço *et al.* 2015) between birds and their potential prey was not evident for most species. While we cannot exclude the possibility of having missed an important $\delta^{15}N$ depleted prey, this is rather unlikely to have happened in all study areas in exactly the same way. Moreover, sampling was carried out based on a thorough literature search on shorebirds diets in order to gather specimens of all prey identified as important. Several other factors may be involved in explaining these results. For instance, in Sidi Moussa, several shorebird species are known to forage in the adjacent salt pans, preying upon chironomidae larvae (Kersten *et al.* 1981; Joulami 2013), which have a significantly $\delta^{15}N$ -depleted signature. Supra-tidal feeding in salt pans at the Tagus estuary (also upon chironomidae larvae) can also be responsible for the

lower $\delta^{15}N$ values of some bird species (Rosa *et al.* 2006; T. Catry, P.M. Lourenço & J.P. Granadeiro, unpublished data), although probably to a lesser extent. Recently, several studies presented evidence for previously undescribed foraging habits of some shorebirds, consuming biofilm (Kuwae *et al.* 2008, Kuwae *et al.* 2012) and seagrass (Robin *et al.* 2013). Such studies highlight gaps in knowledge on the feeding ecology of shorebirds and suggest that 'non-standard' food sources might be more widespread than previously thought. At Banc d'Arguin, for instance, red knots are now known to consume rhizomes of seagrass (J.A. van Gils, pers. comm.) and ongoing analyses showed that dunlin's droppings were mostly empty of other prey apart from a very high number of tiny (<1 mm) ostracods (T. Catry, P.M. Lourenço & J.P. Granadeiro, unpublished data), which have seldom been referred as shorebird's prey (but see Smith *et al.* 2012). Further baseline research on the diet of shorebirds, particularly in poorly known African wintering areas, is clearly needed to help interpreting food web structure and functioning.

Interestingly, our results show that the major organizational patterns of whole food webs scale up to key secondary consumers (shorebirds) suggesting that the latter might represent an adequate representation of the overall structure of tidal food webs.

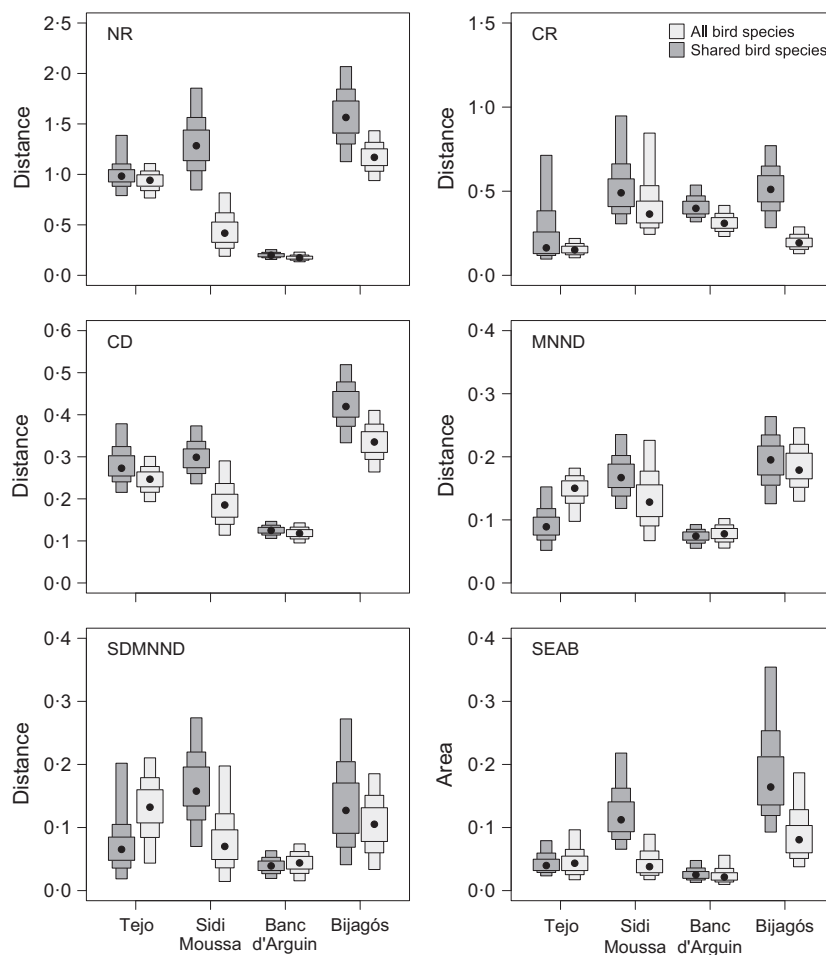


Fig. 4. Bayesian results of the Layman's community-wide metrics and standard Bayesian ellipse area (SEA_B) for (i) entire communities of shorebirds in the four study areas (light grey boxes), and (ii) communities of shorebirds including only species sampled in all the four study areas (dark grey boxes). Black dots represent the mode and boxes present the 50%, 75% and 95% credible intervals. NR = $\delta^{15}N$ range, CR = $\delta^{13}C$ range, CD = mean distance to centroid, MNND = mean nearest neighbour distance, SDMND = standard deviation of mean nearest neighbour distance.

TROPHIC STRUCTURE AND NICHE COMPARISONS AMONG AND WITHIN SHOREBIRD COMMUNITIES

Iso-space metrics estimated for shorebird communities in this study suggest structural differences among areas, which achieved maximum contrast between Banc d'Arguin and Bijagós, the two tropical communities. At Banc d'Arguin, the shorebird community is more 'compact', less diverse and characterized by a shorter trophic length. Interestingly, despite showing the smallest isotopic niche (given by SEA_B), mean niche overlap among species was lower at Banc d'Arguin than at Sidi Moussa and Tejo estuary, suggesting a higher interspecific niche partitioning in Banc d'Arguin. Previous studies have pointed out the unexpected high number of birds in spite of the relatively low standing stocks of macrobenthic fauna at Banc d'Arguin (Engelmoer *et al.* 1984) and have also provided evidence that shorebirds substantially deplete prey stocks during winter (Ahmedou Salem *et al.* 2014). Such evidence suggests that strong interspecific competition might drive resource partitioning at Banc d'Arguin. The same pattern could occur at the Bijagós, where interspecific overlap in niche width was the lowest, as it is believed that tropical systems offer comparatively lower harvestable prey biomass for

shorebirds, potentially constraining their food intake (Piersma *et al.* 2005).

Shorebird species from Sidi Moussa also showed on average, larger niche widths than corresponding ones at Banc d'Arguin and Tejo estuary (Table S5), suggesting a higher degree of intraspecific variability, which might arise via differential habitat use (Quevedo, Svanbäck & Eklöv 2009). As previously mentioned, shorebirds forage both at the intertidal flats and at the salt pans adjacent to the lagoon (Kersten *et al.* 1981; Joulami 2013), and individual variation in the proportions of habitat use (and therefore probably in the proportions of chironomidae larvae consumed) can drive intraspecific niche partitioning.

Bocher *et al.* (2014) described the trophic structure of a wintering shorebird community on the French Atlantic coast suggesting a clear partitioning among four functional groups: worm-eaters (at the highest trophic levels), deposit-suspensivorous mollusc-eaters, suspensivorous mollusc-eaters and opportunistic species. Overall, in our study, red knots and bar-tailed godwits exhibited the lowest levels of niche overlap within local communities. Red knots are almost exclusively molluscivore (Piersma *et al.* 2005), while bar-tailed godwits have been mainly described as worm-specialists (Engelmoer *et al.* 1984; Duijns, Hidayati & Piersma 2013). Diet specialization could thus

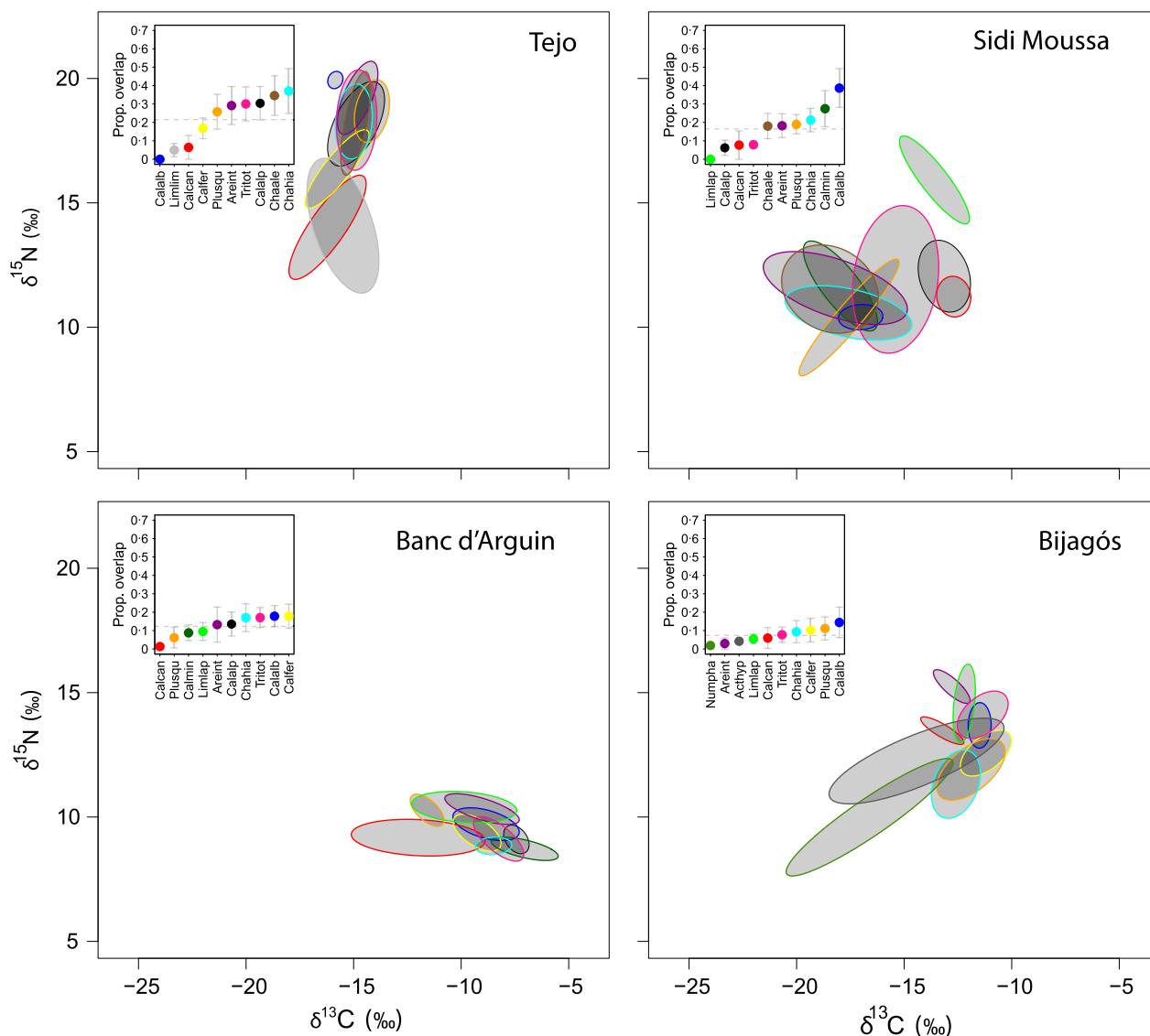


Fig. 5. Overlap in isotopic niches (corrected standard ellipses; SEAC) of individual shorebird species in each of the four study areas. SEAC are not standardized for basal source values, being presented for comparative purposes only within study areas. Inset plots (upper left corner) of each study area represent the mean ($\pm\text{SD}$) niche overlap for each species; the mean overlap for the community is shown by a horizontal grey dashed line.

potentially lead to disparate isotope signatures in comparison with those from more generalist species.

Metrics derived from isotopic data revealed some relevant contrasts in the organization of shorebird communities among the four study areas highlighting the plasticity in the foraging behaviour of species inhabiting areas with distinct environmental conditions. Both population and individual variations in feeding behaviour can cascade up to ecosystem processes, and thus, adaptive behaviour can be an important driver of food web structure (Thompson *et al.* 2012).

Conclusions

Despite the large differences in biotic and abiotic conditions among the studied systems, our study suggests that

food web structure of tidal coastal areas is strongly shaped by external nutrient inputs as well as by the number of trophic pathways of organic matter transfer. A higher number of sources fuelling secondary production promote lower trophic redundancy within the food web which, ultimately, can impact ecosystem resilience. In fact, low trophic redundancy may enhance ecosystem resilience, as the loss of one species can be compensated by another species with the same ecological niche, buffering potential losses in terms of overall ecosystem functioning (Ojwang *et al.* 2010). Studies at a broad geographical scale based on isotope community-wide metrics of coastal systems are not yet available, but it is now recognized they provide major insights into assessing the impact of environmental conditions on the structure of food webs as well as on ecosystem resilience. Identifying and modelling the links

between food web complexity and ecosystem resilience represent a very promising tool in the management of wetland areas across the migratory pathways of shorebirds.

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Data accessibility

Data are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.vg16p> (Catry *et al.* 2015).

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Supporting Information

Additional Supporting information may be found in the online version of this article:

Appendix S1. Methodological protocols.

Fig. S1. Sensitivity analysis on the effects of changing isotope trophic discrimination factors in estimates of the relative contribution of basal food sources to the diet of macroinvertebrates in all study areas.

Table S1. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of basal food sources, producers and consumers (macroinvertebrates) in all study areas.

Table S2. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ signatures of shorebirds (toenails) collected in all study areas.

Table S3. Pair-wise comparisons of Layman's metrics and Bayesian standard ellipse area (SEA_B) between communities of consumers in all study areas.

Table S4. Pair-wise comparisons of Layman's metrics and Bayesian standard ellipse area (SEA_B) between communities of shorebirds in all study areas

Table S5. Estimates of corrected standard ellipse area (SEA_C) and Bayesian ellipse area (SEA_B) for shorebird populations sampled in all study areas.