

Seasonal changes in environmental conditions are not driving migration in seabirds

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Article type : Letter

Abstract

Migration is often thought to be driven by poor environmental conditions during one season and to permit avoidance of harsh weather or resource shortage and tracking of more favourable conditions. Here, we tested this hypothesis in seabirds at the global scale by quantifying niche occupancy during the breeding and non-breeding periods over multiple marine ecoregions and exploring whether the niche dynamics reflects changes in environmental conditions at the breeding and non-breeding grounds. We demonstrate that migratory species exhibit more divergent seasonal niches than resident and dispersive ones. In most cases, migratory status was not related to unavailability of favourable conditions at the breeding or non-breeding grounds, suggesting that niche availability is not the main driver of migration. We hypothesize that this unexpected pattern might arise from strong constraints imposed on seabirds by scarcity of suitable sites breeding which constrain the range of environments available for optimizing reproductive success.

Keywords: Biogeography; Ecological niche; Marine Ecoregions of the World; Niche dislocation; Niche dynamics; Niche overlap; Niche stability; Seasonality

Number of words in the abstract 147

Number of words in the main text 5000

Number of words in the text box no text box

Number of references 35

Number of tables and figures 6

Authors' contributions

CL conceived the ideas and designed the methodology; CL collected and analysed the data; CL and JF wrote the manuscript. Both authors contributed critically to the drafts and gave final approval for publication.

Data Accessibility Statement

All the materials compiled to conduct this work will be made available in the CL Github repository upon publication (<https://github.com/CLambert1>).

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1 Introduction

Environmental conditions faced by living organisms are highly variable in space and time, from hours to decades. Seasonal variability is one of the most predictable dimensions of temporal variability, and is considered one of the main drivers of seasonal movements such as migration (Alerstam et al., 2003; Winger et al., 2019; Dufour et al., 2020). Although today we have a good understanding of many aspects of migration, our general knowledge of how migratory strategy affects the realized ecological niche (Hutchinson, 1957) of species, and in particular the temporal dynamics of species occupancy within their niche, is still limited. The common assumption is that animals engage in seasonal migration from high latitude breeding grounds to avoid bad weather or resource shortage during the unfavourable season, optimising survival by tracking the spatial displacement of optimal energetic conditions (the Green Wave Surfing; Somveille et al., 2019; Winger et al., 2019). This assumption has been supported by recent efforts suggesting that resident species display more pronounced fluctuations in their ecological niche across seasons (Gómez et al., 2016), while migrants preferentially track the same niche (Thorup et al., 2017; Williams et al., 2017; Zúñiga et al., 2017; Zurell et al., 2018; Somveille et al., 2019).

However, most of the research on the relationship between niche characteristics and migration has focused on terrestrial systems, largely on birds (e.g. Laube et al., 2015; Gómez et al., 2016; Thorup et al., 2017; Zurell et al., 2018; Somveille et al., 2019). As a result, whether niche-tracking also tends to characterise migrant species in marine systems is still unknown. Marine pelagic systems are characterised by a strong spatio-temporal structuring (Hunt & Schneider, 1987), and their seasonality globally follows a latitudinal gradient (Supporting Information S1), being strong at temperate and polar latitudes and in large upwellings, but low at equatorial latitudes. Among mobile marine species, seabirds are among the best known groups at the global scale. They exhibit diversified ecological strategies and a wide array of seasonal movements (Box 1, Supporting Information S2). Some species are resident year-round, others disperse widely during the non-breeding period, or engage in basin-scale or pole to pole migrations (Hunt & Schneider, 1987; Gaston, 2004), supposedly to track favourable environmental conditions (Shaffer et al., 2009; Block et al., 2011; Péron & Grémillet, 2013). Seabirds perform some of the longest known migrations, as the 70,900 km of arctic terns (*Sterna paradisea*; Egevang et al., 2010) or the 64,000 km of sooty shearwaters (*Ardenna grisea*; Shaffer et al., 2006).

One of the main characteristics of seabirds that may impact the relationship between niche dynamics and migratory strategy is their particular relationship to land (Gaston, 2004). While feeding within marine waters, seabirds have to go back to land to breed (Schreiber & Burger, 2002). This results in central-place foraging behaviour, wherein foraging movements of breeding birds are spatially constrained by the colony location, and all trips are performed within a specific range around the colony (Gaston, 2004). The availability of breeding sites is also a major constraint, since sites with the required physical and environmental conditions to ensure successful breeding (nest substrate, wind, rain, predators, disturbance...) are quite rare for many species (Coulson, 2002). A colony can successfully establish only if habitats sustaining sufficient resources are available to support the very high energetic demands of densely aggregated breeding individuals (Hamer et al., 2002; Gaston, 2004). On the other hand, when released from reproductive duties, seabirds are also released from the necessity of remaining close to shore and are free to move to virtually any favourable habitat (free-ranging foraging), thanks to their exceptional flight capabilities. Furthermore, seabirds have a broad thermal tolerance range (Schreiber & Burger, 2002), permitting them to live in polar areas and cross the equatorial regions without harm. Several polar species are also able to cope with the polar night and adverse weather of the highest latitudes (some Alcid species for example; Fort et al., 2013).

This work had two objectives which we fulfilled using a biogeographical approach with the monthly presence of 62 seabird species during the breeding and non-breeding periods, across marine ecoregions and at the global scale. First, we aimed to quantify and compare seabird niche occupancy during the breeding and non-breeding periods for different patterns of seasonal movement. More specifically, we tested the hypothesis that, as for terrestrial birds, migrants track their ecological niche throughout the year, while residents switch their niche seasonally. Second, we aimed to test the hypothesis that the niche used by migrants during one season becomes unavailable during the other, suggesting that the avoidance of adverse conditions is a driver of migratory movements and that niche occupancy dynamics is triggered by variations in niche availability. Here, the ecological niche was characterised as the realized part of the fundamental niche resulting from the restrictions imposed on the species distribution in geographical space by the interaction between abiotic, biotic, dispersal and historical factors (Peterson, 2011). Although knowledge regarding seabird distribution and

migration has accumulated at the species level, there has been, to our knowledge, no attempt to concurrently describe the global-scale ecological niches of a wide array of seabird species, ranging from polar to tropical waters. As such, this study is the first integrated analysis aiming to draw perspectives on the link between the seasonal dynamics of the ecological niches of seabirds and migratory status.

2 Material and methods

2.1 Environmental space

The available environmental space was constructed using a PCA based on monthly climatologies of 29 environmental variables characterising the structure of the pelagic ecosystem at the global scale (Supporting Information S1). This technique summarises the environmental conditions to identify environmental structure by maximising data variance. Dynamic environmental variables were derived from global reanalysis of environmental conditions, using the "GLORYS Phys" dataset for sea surface temperature (SST), sea surface salinity (SSS), sea surface current (SSC), sea surface height (SSH), sea ice fraction (SIF), mixed layer depth (MLD); and the "GLORYS Bio" dataset for chlorophyll *a* surface concentration (CHL) and plankton concentration in carbon (PKN). For each month, the mean, minimum and maximum values of SST, SSS, SSC, SSH, SIF, MLD, CHL and PKN were summarised over the complete available period (2007-2017) to compute monthly climatologies. Minimum and maximum were considered in addition to the mean to take into account the temporal variability of environmental conditions within each month. The mean solar radiance (UVB) was used as a proxy for day length. UVB was extracted from the "Global UV-B radiation dataset for macro-ecological studies", using the monthly climatologies constructed from daily measurements summarised into monthly means over the period of 2004-2013. As UVB is null over polar areas during winter, we replaced the pixels with no values with zero values, to avoid removing these areas from the analysis. Similarly, SIF values were set to zero in all pixels without sea ice. Two static variables, bathymetry and roughness, were extracted from the BioORACLE database. All variables were resampled at a 1° resolution, centred and scaled before performing the PCA. CHL and PKN were logged. Each 1° cell was considered 12 times in the analysis (one per month). The PCA was computed in R version 3.5.1 with the FactoMineR package (Husson et al., 2016; R Core Team, 2018). A single PCA was performed to ensure comparison of niche dynamics across species.

One inherent risk in characterizing the realised niche is the use of uninformative or irrelevant environmental gradients, *i.e.* with very small effects on species fitness, thereby impairing relevant assessment of niche dynamics. To reduce this risk, we considered only environmental variables with recognized importance to seabird ecology. These environmental parameters can have direct effects on bird physiology (temperature, salinity, solar radiance) or diet (plankton concentration). However, most of them are important to seabirds as proxies of either prey availability (MLD, chlorophyll and plankton concentration) or oceanographic processes favouring prey aggregation (upwellings, eddies, river plumes, tidal fronts, described by roughness, SST, SSS, SSC and SSH; Weimerskirch, 2007; Wakefield et al., 2009). We incorporated minimum and maximum monthly values to include a full description of temporal variability and potential effects of extremes in the analysis: the monthly mean of one environmental parameter might not constrain the presence of a species at a given time, but its maximum value might impair species survival through threshold effects (e.g. Šímová et al., 2011).

2.2 Species seasonal distributions and species phenology

Sixty-two species of flying seabirds from seven families were included (Supporting Information S2): 10 *Alcidae* species, 10 *Diomedidae*, four *Fregatidae*, two *Laridae*, three *Phaethontidae*, 23 *Procellariidae* and 10 species of *Sulidae*. Their presence was assessed during the breeding and non-breeding periods across the Marine Ecoregions of the World (Spalding et al., 2007, 2012), classifying the coastal, shelf and surface pelagic waters into biogeographic ecoregions. Here, we simplified the original dataset from 269 to 96 ecoregions to match the resolution of environmental conditions (Supporting Information S1). Breeding and non-breeding distributions, breeding periods and migratory strategies were determined for individual species from the literature, and from the BirdLife Data Zone when the coded ranges were consistent with knowledge from the literature (see Supporting Information S2 for detailed references). We only used species for which knowledge on seasonal movements was available during both the breeding and non-breeding periods over a set of colonies representative of the entire distribution range. Four seasonal movement patterns were considered: migrant, partial migrant, dispersive,

resident. 45% of species were migratory (28 species), 24% dispersive (15 species), 16% resident (10 species) and 15% partially migratory (9 species).

2.3 Seasonal dynamics of niche occupancy

The ecological niche of seabirds during the breeding period is composed of two subniches: the at-sea and the nesting subniches. The at-sea subniche is directly related to the survival of immature and adult individuals, and partly to chick survival, and as such might have the larger effect on the overall species growth rate. The nesting subniche is characterised by the set of environmental conditions occurring at the reproductive sites on land (wind, rain, snow, predatory pressure), and impacts the species growth rate by directly conditioning the survival of the brood (but not that of adults). This terrestrial subniche being by definition deserted during the non-breeding period, the breeding and non-breeding niches are always partially divergent. The overall reduced availability of this nesting subniche in the geographical space combined with central-place foraging constraints makes large portions of the ocean inaccessible that would otherwise be included in the fundamental or potential niches. Here, we focused on the at-sea subniche resulting from these accessibility limitations.

We analysed the seasonal niche dynamics of seabirds following four steps and using the R package *ecospat* (Broennimann et al., 2012; R Core Team, 2018). (1) Species presence in ecoregions during breeding and non-breeding periods were projected over the environmental space depicted by the first two PCA dimensions. (2) Occurrences on the gridded environmental space were converted into densities, then smoothed using a kernel function to describe species' seasonal niches. (3) Niche dynamics were quantified with four metrics (Figure 1a): (A) Niche overlap between seasons was estimated using the Schoener's D on species' occupancies in the environmental space, correcting for environmental availability, by dividing the density of occurrence in each niche by the density of the environment in the entire environmental space; (B) Breeding specificity was quantified as the proportion of occurrences in the breeding niche located in environmental conditions not occupied during the non-breeding season; (C) Non-breeding specificity was the proportion of occurrences in the non-breeding distribution located in environmental conditions not occupied during the breeding season; (D) Stability of the non-breeding niche was the proportion of occurrences in the non-breeding distribution located in environmental conditions also occupied during the breeding season. The four metrics ranged from 0 to 1.

We formulated five theoretical patterns that could characterise seasonal niche dynamics (Figure 1), from near-complete overlap (*i.e.*, niche tracking) to complete dislocation (*i.e.*, niche switching). Extreme niche tracking behaviour would result in a strong overlap between seasonal niches, low breeding and non-breeding specificities but high stability (Figure 1B). Extreme niche switching behaviour would result in low to no overlap, with high breeding and non-breeding specificities but low stability (Figure 1B). We tested for the equality of medians across seasonal movement types for each metric, comparing all types together and then each pair separately if the first test was significant. A Kruskal-Wallis test was used due to the non-normality and non-homogeneity of variances.

Finally, we computed the difference between the average position of species occurrences across PCA dimensions during the breeding and non-breeding periods to investigate the orientation of seasonal shifts in niche position. We also computed the difference in niche breadth between periods (niche breadth was the difference between the minimum and maximum positions of species occurrences on the PCA dimensions).

2.4 Seasonal changes in niche availability

To test if migration was triggered by the avoidance of adverse conditions during the non-breeding period, we simulated (1) species residency at the breeding grounds by considering species to range only in the breeding grounds during the non-breeding period, and (2) residency in the non-breeding grounds by considering species to range only in the non-breeding grounds during the breeding period. If the assumption that migration is driven by avoidance of adverse conditions was true, there should be strong seasonal differences due to changing environmental conditions between the two periods.

Overlap, breeding specificity, non-breeding specificity and stability were computed for the two simulated residencies. We then compared the metrics obtained with the true distribution and the two simulated residencies separately for each movement type using a paired Wilcoxon test, and visually inspected the deviation of observed niches from simulated residencies for each species.

3 Results

3.1 Environmental space

The first two PCA dimensions were retained to define the environmental space, explaining 56.3% of the total variance of the dataset (Supporting Information S3A). The first dimension, explaining 34.8% of the variance, represented a gradient from areas of high temperature, high plankton concentration and high sea surface height to polar areas with an important sea ice fraction. The second dimension, explaining 21.5% of the variance, corresponded to a productivity gradient.

3.2 Species seasonal distributions

A large number of species were distributed in the Indian Ocean, south Pacific Ocean, California Current System and in subantarctic waters during their breeding periods (with up to 14 species occurring in the southern Indian Ocean; Figure 2A and Supporting Information S3B). The only ecoregions not used by any species during their breeding period were the Black Sea, the northern Bay of Bengal and the Arabian Gulf. During their non-breeding period, a majority of seabirds were found in the Atlantic Ocean (north and south), southern Indian Ocean, northern Pacific Ocean and over the southern tropical convergence of the Pacific Ocean (with up to 13-15 species in the California Current, north Atlantic Transitional zone and southern Indian Ocean; Figure 2B and Supporting Information S3B). As for the breeding period, no species occupied the northern Bay of Bengal and the Arabian Gulf during the non-breeding period.

3.3 Niche dynamics under true distribution

All theoretical patterns of seasonal niche dynamics except for complete dislocation (Figure 1B) were identified in at least one of the 62 studied species. The overlap between seasonal niches of all species was high, with an average of 0.68 ± 0.21 (mean \pm standard deviation; range: 0.24–1.00; Table 1). Overall, breeding specificity and non-breeding specificity were low, averaging 0.05 ± 0.08 (from 0.00 to 0.37) and 0.06 ± 0.11 (from 0.00 to 0.59), respectively. Niche stability was strong with an average of 0.94 ± 0.11 (from 0.41 to 1.00).

Kruskal-Wallis tests confirmed that niche dynamics strongly depended on the migratory status (Figure 3 and Table 1; Supporting Information S4), as at least one of the statuses had a median differing from the others for each of the four metrics (overlap: $p < 0.01$; breeding specificity : $p = 0.03$, stability and non-breeding specificity: $p < 0.01$). Pairwise tests showed that migrant species had a significantly lower overlap between niches than resident, partial migrant and dispersive species ($p < 0.01$, $p = 0.03$, $p < 0.01$, respectively; Figure 3A and Table 1). Migrants also had higher breeding specificity than dispersive species ($p < 0.01$; Figure 3B and Table 1). Migrant and partial migrants exhibited lower stability and higher non-breeding specificity than resident and dispersive species (Figures 3C, D and Table 1): $p < 0.01$ for migrant-dispersive and migrant-resident comparisons, $p = 0.02$ for partial migrant-dispersive and $p < 0.01$ for partial migrant-resident.

The difference in niche positioning and breadth between the two seasons also varied according to migratory status (Figure 4A and Supporting Information S4). Dispersive species did not shift their niches between seasons (null differences for the two dimensions, Figure 4A) but exhibited wider niches on the second dimension during the breeding period (Figure 4B). Resident species experienced, on average, warmer and saltier (dimension 1) but also more productive waters (dimension 2) during the breeding period compared to the non-breeding one (positive differences for both dimensions; Figure 4A). They displayed no difference in niche breadth between breeding and non-breeding niches on the second dimension, but wider breeding niches on the first one (Figure 4B). Migrant and partial migrant species experienced more productive waters during the breeding period (dimension 2, Figure 4A). They shifted niche averaged positioning between season for the first dimension as well, but in both directions with species experiencing warmer and saltier waters during the breeding season or the opposite. Both groups exhibited non-breeding niche wider than the breeding one (Figure 4B), on both dimensions for migrants but mostly on the first dimension for partial migrants.

3.4 Niche dynamics under simulated residency

Niche dynamics were similar when residency was simulated in the breeding and non-breeding ranges for resident and dispersive species (non-significant differences; Figure 3, Supporting Information S4). Partial migrants exhibited similar niche

overlap and breeding specificity if remaining resident in the breeding or non-breeding areas (non-significant differences), but exhibited smaller ranges of niche stability and non-breeding specificity under simulated residency than for the true seasonal distribution ($p = 0.04$ for stability and non-breeding specificity; Figure 3). Simulated seasonal niches for migrants resident in either the breeding or non-breeding ranges were more similar across seasons than the observed seasonal niches of migrants (Figure 3). For migrants, the overlap increased to values similar to that of the other groups for both simulated residencies ($p < 0.01$ for residency in breeding areas and in non-breeding areas), while breeding specificity was strongly reduced compared to the true distribution (difference only significant for residency in non-breeding area, $p = 0.01$). Stability and non-breeding specificity remained the same in the case of residency in the breeding range ($p > 0.05$), but stability was larger and non-breeding specificity smaller in the case of residency in the non-breeding range ($p < 0.01$ in both cases).

Visual inspection of the relationships between metrics obtained from the true distribution and simulated residency (Figure 5) confirmed that migrants deviated more from equivalence (1:1 line) than others species (except for two partial migrant species, the yelkouan (*Puffinus yelkouan*) and Balearic (*P. mauretanicus*) shearwaters). The overlap between true breeding and non-breeding niches was lower for migrants than when residency was simulated in the breeding and non-breeding ranges (the largest deviations were observed for the Antarctic (*Pachyptila desolata*) and slender-billed (*P. belcheri*) prions; Figure 5A). Yet, some species (including dispersive and partial migrants) exhibited the opposite pattern, with a true overlap larger than under simulated residency, such as the yelkouan shearwater, the Chatham albatross (*Thalassarche eremita*), the black-footed albatross (*Phoebastria nigripes*) and the Barolo shearwater (*Puffinus baroli*). The majority of species had breeding specificity similar to the one obtained from simulated residency in the breeding and non-breeding ranges (Figure 5B), but a set of species exhibited strong deviations from simulated residency: breeding niches were either more different (higher breeding specificity; in particular the sooty and short-tailed (*Ardeana tenuirostris*) shearwaters) or more similar (lower breeding specificity; yelkouan and Balearic shearwaters) than non-breeding niches. There was less deviation from what would occur under simulated residency for stability and specificity of non-breeding niches (Figures 5C, D), but niche stability was still lower and specificity higher for migrants (*i.e.*, non-breeding niches differed more from breeding niches than under simulated residency). A set of three species stood out, exhibiting much lower stability and much higher expansion than under simulated residency (higher dissimilarity in seasonal niches): the Antarctic and slender-billed prions (migrants) and the Balearic shearwater (partial migrant).

4 Discussion

4.1 Seasonal dynamics of ecological niches

Our quantification of the ecological niche dynamics of 62 seabird species demonstrated that they all tracked their ecological niche between seasons to some extent, with strong niche overlap (68% on average) between the breeding and non-breeding periods. Thus, there was a high stability of environmental conditions between the two niches: on average, 94% of the non-breeding niche was included in the breeding niche and only 5% of conditions encountered in the breeding niche were not encountered in the non-breeding niche (breeding specificity).

Seasonal niche dynamics nonetheless varied between species with different migratory status. Resident and dispersive species had an average overlap $>80\%$ between their seasonal niches, with almost complete stability of environmental conditions between the breeding and non-breeding niches. Resident and dispersive species were distributed mainly at low latitudes (boobies, tropicbirds and frigatebirds) in the least seasonal environments, where encountered environmental conditions barely change across the year, explaining this strong stability. However, some resident and dispersive species exhibiting niche tracking were also distributed in highly seasonal subpolar to polar waters. This was the case for the black guillemot (*Cephus grylle*), the marbled murrelet (*Brachyramphus marmoratus*), the light-mantled albatross (*Phoebastria palpebrata*), the sooty albatross (*Phoebastria fusca*), the Indian yellow-nosed albatross (*Thalassarche carteri*), the northern fulmar (*Fulmarus glacialis*), the Barolo shearwater and the blue petrel (*Halobaena caerulea*). These species exhibited similar breeding and non-breeding niche contours, but their highest densities were located in different parts of their niches due to environmental seasonality. We can thus propose that these species have developed strategies other than migration to cope with unfavourable environmental conditions (Shaffer et al., 2001; Fort et al., 2013; Winger et al., 2019).

Partial migrant species exhibited an intermediate pattern between resident/dispersive and migrant species, as found

for the thermal niche by [Dufour et al. \(2020\)](#). The seasonal niche overlap of partial migrants was lower than in resident and dispersive species but larger than in migrants. Stability and non-breeding niche specificity of partial migrants were similar to that of migrants, but their breeding specificity was similar to resident and dispersive species. This pattern indicates that the non-breeding niche incorporates and expands the breeding one, as confirmed by the difference in niche breadth between seasons. As a result, partial migrants do not switch, but rather expand, their ecological niche during the non-breeding period (third theoretical niche dynamics in Figure 1B). The intermediate pattern observed in partial migrants might originate in the migratory portions of the population exhibiting niche switching, while the resident portions track the same niche year-round, although testing this hypothesis would require examining the niche dynamics of the migrant and resident portions of the population separately.

Contrary to studies showing niche-tracking migrants ([Gómez et al., 2016](#); [Zurell et al., 2018](#); [Somveille et al., 2019](#)), the migratory species included in our study displayed more divergent breeding and non-breeding niches than other species ([Dufour et al., 2020](#)). They exhibited the lowest overlap coupled with the lowest stability of the environmental conditions between seasonal niches, and the largest breeding niche specificity. Migrants also exhibited the largest differences in niche breadth between seasons. These species engaged in short to long-range migrations, including basin-scale, trans-equatorial migrations. It has previously been suggested that long-range migration in seabirds might be linked to niche tracking, allowing individuals to follow an endless summer, such as in sooty shearwaters in the Pacific Ocean ([Shaffer et al., 2006](#)) or in Scopoli shearwaters (*Calonectris diomedea*) from the Mediterranean Sea to the equatorial Atlantic ([Péron & Grémillet, 2013](#)). The present results caution against considering niche tracking a golden rule for marine migrants, given the stronger level of niche divergence observed in migrant species when considering a large set of environmental conditions, rather than productivity only, as has previously been done. Some trans-equatorial migrants did exhibit similar (but not identical) niches between the breeding and non-breeding seasons, despite performing long-range, basin-scale migrations: Chatham albatross, Buller's albatross (*Thalassarche bulleri*), Cook's petrel (*Pterodroma cooki*), Deserta's petrel (*Pterodroma deserta*). Yet, others species performing similar basin-scale migrations exhibited some of the most divergent seasonal niches among studied species: sooty shearwater, great shearwater (*Ardenna gravis*, unlike in [Shaffer et al., 2006](#)), and short-tailed shearwater.

4.2 Environmental drivers of seabird migration

Our results point towards a more complex pattern than migrant tracking favourable conditions, as migrant species exhibited some variation in their niche occupancy across seasons. However, the question remains open as to whether migration is triggered by avoidance of unfavourable conditions, which could optimise the individual survival during the non-breeding period ([Alerstam et al., 2003](#); [Shaw & Couzin, 2013](#); [Somveille et al., 2019](#); [Winger et al., 2019](#)). Here, we tested this hypothesis by simulating the residency of seabirds in their breeding and non-breeding grounds. If migration was triggered by favourable conditions becoming unavailable, simulated residency should show important variations in niche occupancy.

This was, however, found for two partial migrant species only, the yelkouan and the Balearic shearwaters. Both species breed in the Mediterranean Sea from October to May/July ([Guilford et al., 2012](#); [Raine et al., 2013](#)). Environmental conditions encountered during this higher productivity period changed drastically during the non-breeding period (see Supporting Information S4), and both species cope with this change by performing short and medium scale migrations to track their niche, to the eastern Mediterranean, Black Sea (yelkouan shearwater; [Raine et al., 2013](#)) and the Bay of Biscay (Balearic shearwater [Guilford et al., 2012](#)). The environmental envelop ensuring individual survival became too scarce to ensure the maintenance of the complete population within the breeding range, eventually driving the migration of a large portion of the populations.

Conversely, the stand-out result arising from this work is that, for all other species and whatever their migratory strategies, environmental conditions used during the breeding and non-breeding periods remained available during the other period. Migrants exhibited stronger seasonal variation in niche occupancy when migrating than if they stayed in either the breeding or non-breeding grounds. Thus, our results suggest that the unavailability of favourable conditions is not a primary driver of migration, contrary to what is commonly suspected.

This striking result is opposite to what was found in terrestrial birds ([Laube et al., 2015](#); [Gómez et al., 2016](#); [Thorup et al., 2017](#); [Zurell et al., 2018](#)) and, opens the question as to why seabirds engage in migration if favourable conditions remain available? For a migratory strategy to be viable, it must come with a fitness benefit, either through enhanced survival or improved reproductive success. As mentioned above, one of the main characteristics of seabirds is their reliance

on land for reproduction. This characteristic entails strong constraints on species distribution in that it induces central-place foraging behaviour, and necessitates sites suitable enough to support reproduction in mostly densely aggregated colonies and permit the survival of both adults and chicks. During the breeding period, aggregations of individuals around colonies induce the strongest level of competition faced by seabirds during their phenological cycle (Gaston, 2004), and this intense competition occurs during the most energy-demanding period. However, once the breeding duties are completed, seabird energetic requirements drop (no chick to rear) and the central-place foraging constraint is released. This results in a dilution of intra-specific competition during the non-breeding period, but also in the possibility for individuals to move to more favourable areas otherwise inaccessible during the breeding period.

We can then reasonably suggest that the larger shift observed in the seasonal niches of migrating seabirds compared to resident ones reflects the fact that individuals move between areas containing the environment that optimises reproductive success and areas optimal for the free-ranging period. The large-scale seasonal movements of seabirds are thus not driven by niche availability alone but rather by the combination of biological (reproductive duty) and environmental constraints (breeding site availability) imposed during the breeding period which eventually lead species to switch their niche between seasons (Shaw & Couzin, 2013; Winger et al., 2019). Our results demonstrate that migrant species do use, on average, more productive areas during the breeding period, which is consistent with the necessity of reproducing in an environment allowing sustenance of the very high energetic needs of breeding individuals, despite the high levels of competition occurring at colonies. On the other hand, migrants used less productive areas during the non-breeding period. This result is consistent with a decrease in energy requirements and the removal of central-place foraging constraints permitting individuals to alleviate their reliance on the most productive systems and disperse across wider areas, thereby diluting intra-specific competition.

To conclude, we, for the first time, describe the global seasonal dynamics of a wide array of seabird species, ranging from polar to tropical waters. Our biogeographical approach allowed us to explore the interplay between the ecological niche and seasonal migration strategies. We demonstrate that all seabirds are niche trackers, yet contrasting dynamics occurred depending on seasonal movement types. Resident and dispersive seabirds displayed high levels of niche tracking throughout the year, regardless of the environmental seasonality, while migrants exhibited more divergent seasonal niches. In most cases, breeding and non-breeding niches of migrants were still available during the other period, suggesting that migration is not primarily driven by availability of the favourable niche. This result contrasts with previous results obtained on terrestrial systems, and might originate from the particular biological constraints experienced by seabirds. Specifically, seabird migration might in part be driven by the scarcity of breeding sites, which may force individuals to move between areas where the environment allows for optimization of reproductive success and non-breeding grounds that are optimal during the free-ranging period. Determining whether the difference between our results and earlier work derives from intrinsic differences between oceanic and terrestrial systems would require performing a similar analysis on other marine groups including highly migratory species, such as cetaceans, pinnipeds, sharks or other large fishes.

Acknowledgements

We warmly thank Auriane Virgili for constructive discussion about the topic and suggestions that improved the work. We also are deeply grateful to Drs Melissa and Andrea Grunst for proof-reading of the english as well as to Prof. Allen Hurlbert and two anonymous referees for constructive comments on previous versions of this manuscript.

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Tables

Table 1. Niche dynamics metrics from true distributions (expressed as mean \pm standard deviation [min; max]) for all species, dispersive species, migratory species, partially migratory species and resident species.

	All species	Dispersive	Migrant	Partial Migrant	Resident
Number of species	62	15	29	8	10
Overlap	0.68 ± 0.21 [0.24; 1.00]	0.83 ± 0.19 [0.43; 1.00]	0.55 ± 0.15 [0.24; 0.80]	0.68 ± 0.17 [0.32; 0.91]	0.81 ± 0.17 [0.48; 1.00]
Breeding niche specificity	0.05 ± 0.08 [0.00; 0.37]	0.02 ± 0.04 [0; 0.14]	0.08 ± 0.10 [6.19×10^{-6} ; 0.37]	0.02 ± 0.03 [0.00; 0.07]	0.04 ± 0.09 [0; 0.30]
Stability	0.94 ± 0.11 [0.41; 1.00]	0.99 ± 0.01 [0.97; 1.00]	0.90 ± 0.13 [0.41; 1.00]	0.92 ± 0.11 [0.65; 1.00]	0.99 ± 0.02 [0.96; 1.00]
Non-breeding niche specificity	0.06 ± 0.11 [0.00; 0.59]	0.01 ± 0.01 [0.00; 0.03]	0.10 ± 0.13 [1.94×10^{-3} ; 0.59]	0.08 ± 0.11 [5.64×10^{-4} ; 0.35]	$8.90 \times 10^{-3} \pm 0.15$ [0.00; 0.04]

Figures

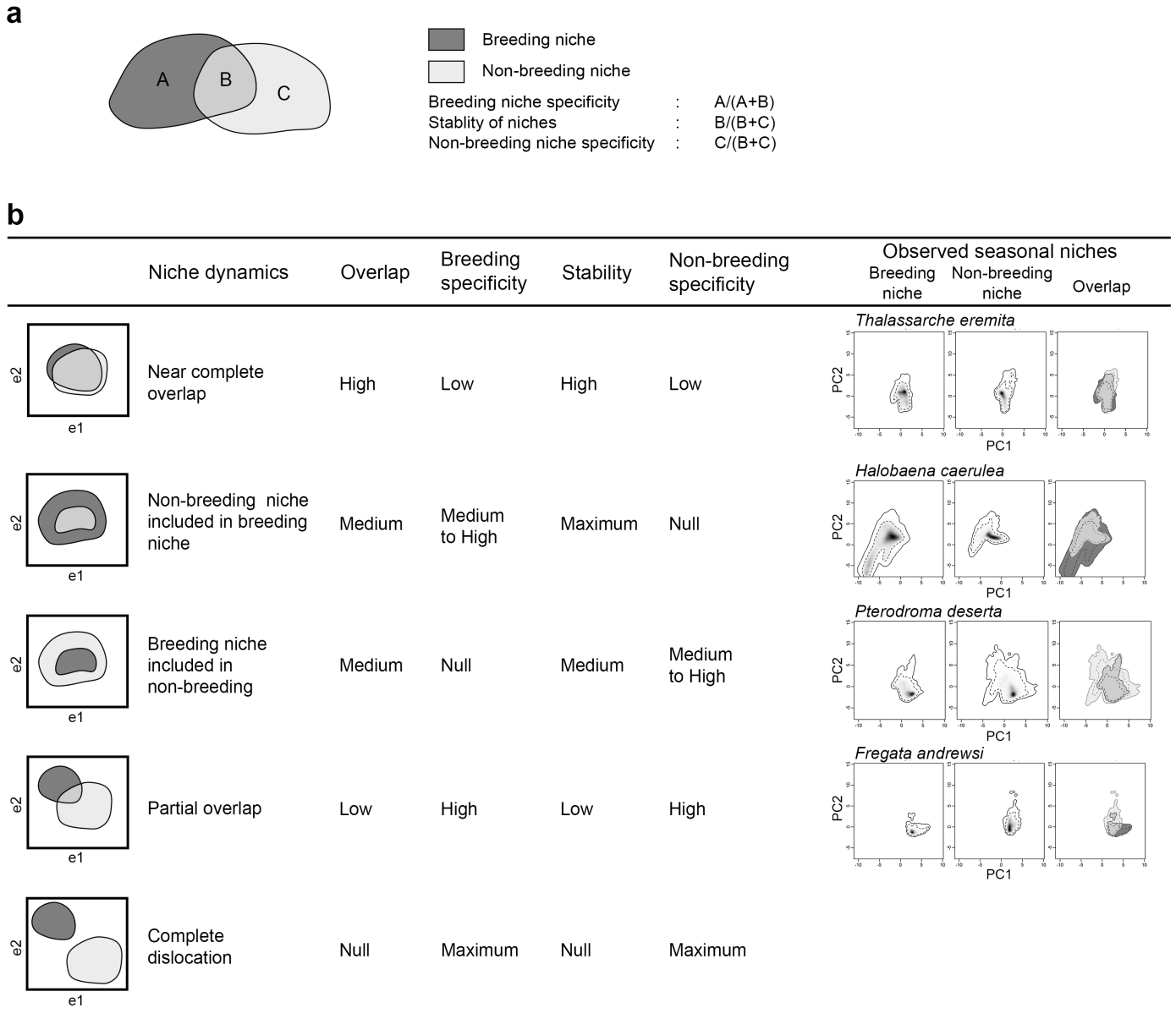
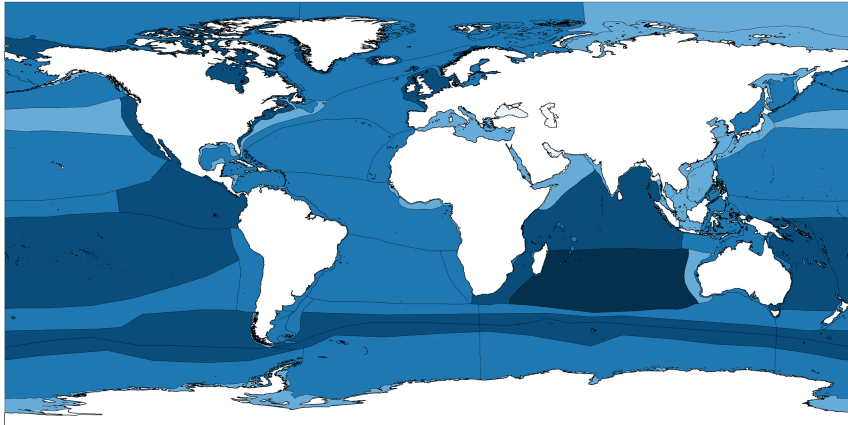
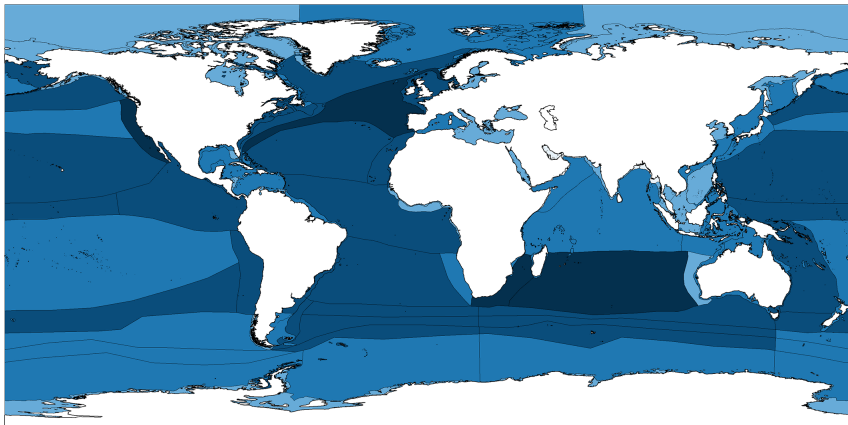


Figure 1. (a) - Seasonal niches projected on environmental spaces and the four metrics derived from their comparisons: niche overlap, breeding specificity (portion of the niche occupied only during the breeding season), niche stability (portion of the niche occupied in both seasons) and non-breeding specificity (portion of the niche occupied only during the non-breeding season); (b) - Five different possible niche dynamics along the continuum from niche tracking to niche switching, and their resulting comparison metrics (overlap, breeding specificity, stability and non-breeding specificity), with examples from observed seabird seasonal niches. One species is shown as an example for each category (Chatham albatross *Thalassarche eremita*, blue petrel *Halobaena caerulea*, Desertas petrel *Pterodroma deserta* and Antarctic prion *Pachyptila desolata*). The breeding (left panel) and non-breeding (centre panel) niches are shown displaying the densities of presence inside the niche as shaded grey. The overlap between the two niches is shown in the right panel, with breeding niche in dark grey, non-breeding niche in light grey and overlap in mid-tone grey. The solid contour lines depict 100% of the available environment, the dashed contour lines 50% of the most common background environment. There was no seabird species exhibiting complete dislocation of seasonal niches.

a - Breeding



b - Non breeding



Number of species



Figure 2. (a) - Number of species present in each Marine Ecoregion of the World (Spalding et al., 2007, 2012) during their breeding periods and (b) - during their non-breeding periods. Note that the breeding and non-breeding periods do not necessarily overlap among species present in similar ecoregions, meaning they are not necessarily present at the same time.

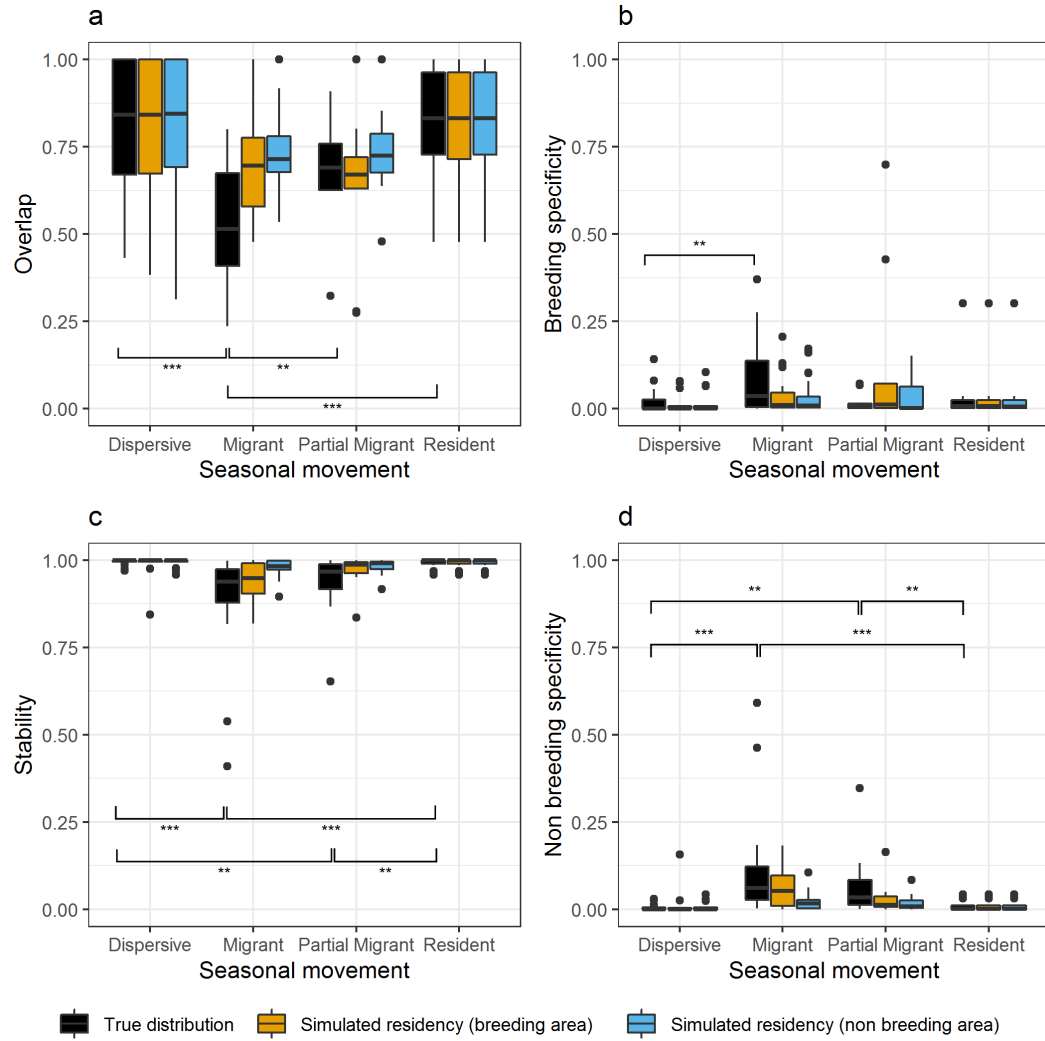


Figure 3. (a) - Species niche overlap, (b) - breeding niche specificity, (c) - stability of niches and (d) - non-breeding niche specificity for each type of seasonal movement pattern for the true distribution (observed niche, in black), simulated residency in breeding area (orange) and simulated residency in non-breeding area (blue). The highlighted pairs of seasonal movement patterns are those exhibiting significantly different medians (for true distributions only) as determined by Kruskal-Wallis tests, with the corresponding significance levels below.

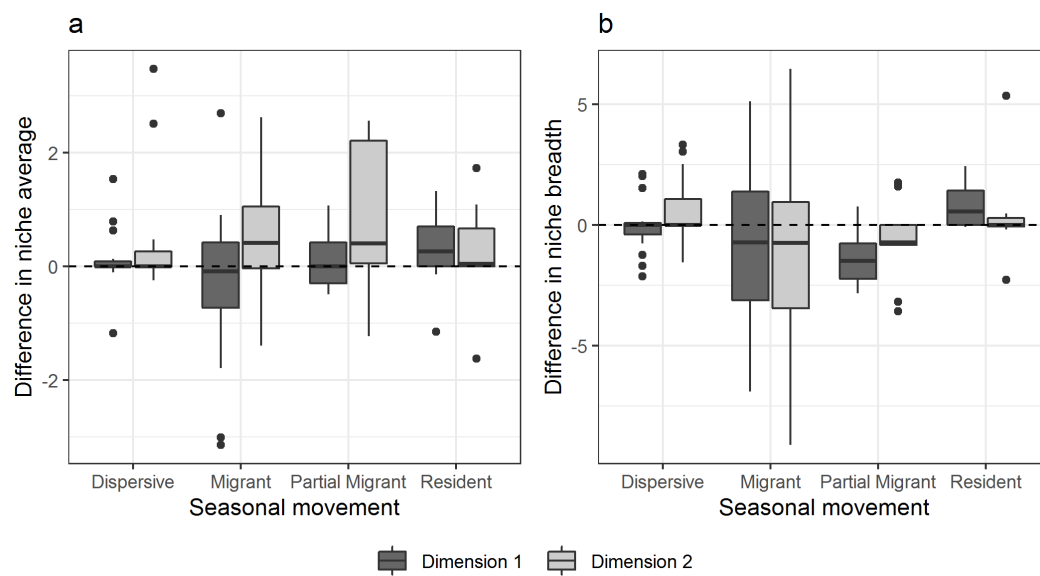


Figure 4. (a) - Differences in averaged position of species occurrences on PCA dimensions 1 and 2 between the breeding and non-breeding periods. Positive differences correspond to warmer, saltier and shallower waters (dimension 1) or more productive waters (dimension 2) during the breeding period compared to the non-breeding one. (b) - Differences in niche breadth between the breeding and non-breeding periods. Positive differences indicate a wider breeding niche compared to the non-breeding one.

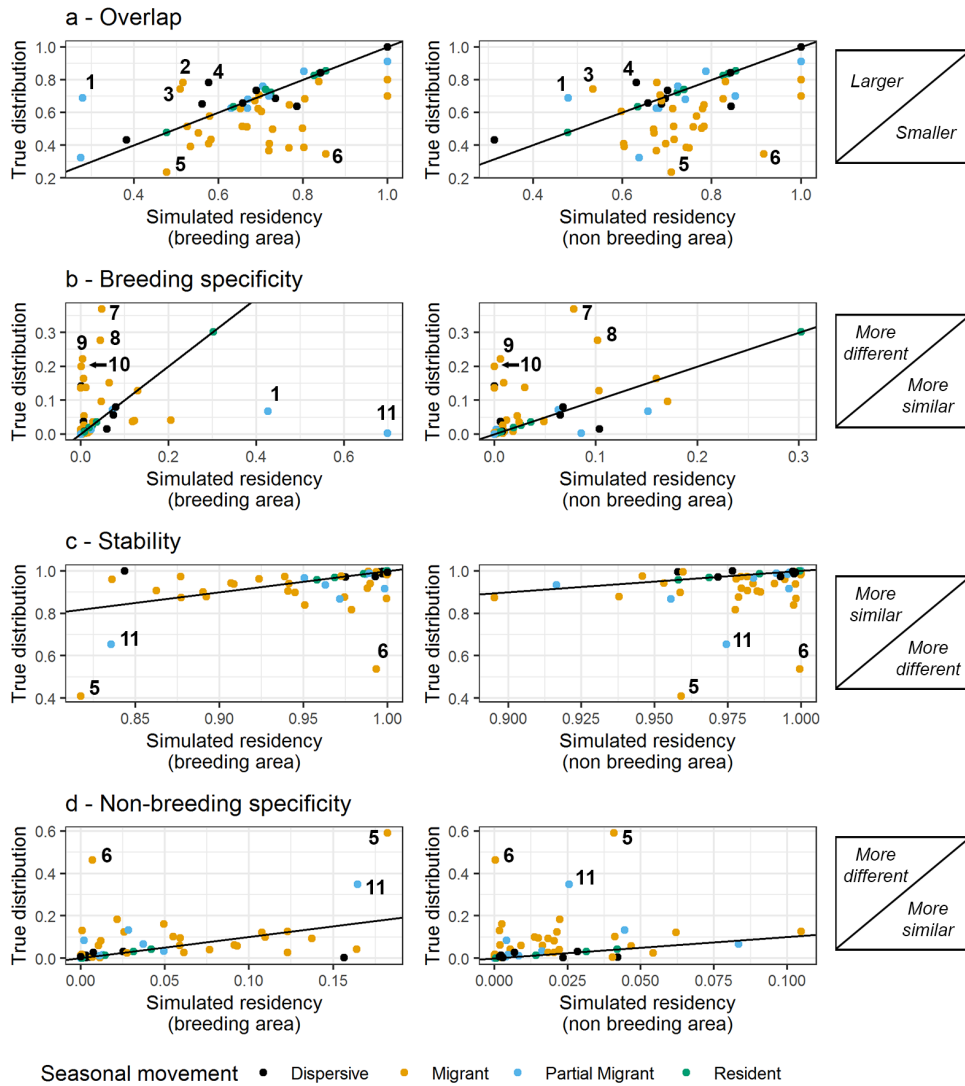


Figure 5. Relationship between observed niche (true distribution) and simulated niche (left: simulated residency in breeding area; centre: simulated residency in non-breeding area). (a) - Overlap of seasonal niches: species occurring above the line display stronger overlap in the observed distribution than under simulated residency (right panel). (b) - Breeding niche specificity: species occurring above the line have conditions encountered during the breeding period that differ more from conditions encountered during the non-breeding period than under simulated residency (right panel). (c) - Stability of seasonal niches: species occurring below the line have conditions encountered during the non-breeding period that differ more from conditions encountered during the breeding period than under simulated residency (right panel). (d) - Non-breeding niche specificity: species occurring above the line have conditions encountered during the non-breeding period that differ more from conditions encountered during the breeding period than under simulated residency (right panel). Some species displaying contrasting behaviours are specified: 1 - Yelkouan shearwater (*Puffinus yelkouan*); 2 - Chatham albatross (*Thalassarche eremita*); 3 - Black-footed albatross (*Phoebastria nigripes*); 4 - Barolo shearwater (*Puffinus baroli*); 5 - Antarctic prion (*Pachyptila desolata*); 6 - Slender-billed prion (*Pachyptila belcheri*); 7 - Sooty shearwater (*Ardenna grisea*); 8 - Short-tailed shearwater (*Ardenna tenuirostris*); 9 - Black-legged kittiwake (*Rissa tridactyla*); 10 - Christmas frigatebird (*Fregata andrewsi*); 11 - Balearic shearwater (*Puffinus mauretanicus*).