Joint seasonality in geographic and ecological spaces, illustrated with a partially migratory bird

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Abstract

As most species live in seasonal environments, considering varying conditions is essential to understand species dynamics in both geographic and ecological spaces. Both resident and migratory species need to contend with seasonality, and balance settling in favorable areas with tracking favorable environmental conditions during the year. We present an exploratory framework to jointly investigate a species' niche in geographic and ecological spaces, applied to Wood Storks (*Mycteria americana*), a partially migratory wading bird, in the southeastern U.S. We concurrently described monthly geographic distributions and climatic niches based on temperature and precipitation. Geographic distributions of Wood Storks were more similar throughout the year than climate niches were, suggesting that birds stay within specific areas seasonally, rather than tracking areas of similar climate. However, Wood Storks expressed consistent selection of warm areas during the winter, and wet areas during the summer, indicating that the selection of seasonal ranges may be directly related to environmental conditions across the entire range. Our flexible framework, which simultaneously considered geographic and environmental spaces, suggested that tracking climate alone did not explain seasonal distributions of Wood Stork in breeding and non-breeding areas.

Keywords: climatic niche, ecological niche, kernel overlap, range, Wood Stork

1 Introduction

At the core of ecology is the question of where do animals live? Early on, ecologists acknowledged the dual nature of this issue, by investigating species ranges, i.e. their location in geographic space (Candolle, 1855; Darwin, 1859; Wallace, 1876), and species ecological niches, i.e. their location in ecological space (Grinnell, 1917; Hutchinson, 1957). More recent is the joint investigation of the effect of a change in one space on the other—e.g. how range constraints caused by migration or breeding affect a species' niche (Kearney and Porter, 2009), or how climate change may affect species' range limits, (Chen et al., 2011). However, the dynamic nature of both spaces in time—i.e. their *seasonality*—often goes unacknowledged, despite the fact that most species live in seasonal environments (Fretwell, 1972), with strongly cyclic variations in resource availability and conditions throughout the year. Here, we illustrate the use of a generalized framework for joint seasonality in geographic and ecological (specifically climatic) spaces, with the case of a partially migratory bird, Wood Storks (*Mycteria americana*) in the Southeastern United States.

Movement has evolved as the primary means to manage heterogeneous environments in space or in time (Nathan et al., 2008). Motile animal species can be placed on a gradient from sedentary to migratory (Chapman et al., 2011; Cagnacci et al., 2011), with direct implications for seasonal overlap, both in geographic and ecological spaces. Sedentary species should exhibit a high consistency in their range, but will experience environmental seasonality, resulting in low ecological similarity throughout the year. On the other hand, migration is a dramatic response to seasonal environmental change (Dingle and Drake, 2007), which leads to two distinct seasonal ranges. As a consequence, each stage should be highly consistent in both geographic and ecological spaces, but with very little similarity between seasons. Some species also migrate "in place", e.g. through altitudinal migration (i.e. migratory range shifts along an elevation gradient, Zweifel-Schielly et al., 2009). These species mostly stay within their global range year-round, while buffering for seasonally varying conditions to some extent, and should thus present intermediate characteristics in terms of similarity in

geographic and ecological spaces.

Finally, it has been recognized that many species express a form of partial migration (a fraction of the population is migratory, while the other part remains resident, Chapman et al., 2011), or facultative migration (individuals that may or may not migrate in a given year, Newton, 2012). Partial or facultative migrants pose a conundrum, as some individuals will experience different ranges and different environmental conditions than others during part of the year or in different years. This plasticity allows facultative migrants to pick and choose when to migrate in response to environmental conditions or internal state, as opposed to presumably more hard-wired obligate migrants. In the case of partial migration, we thus expect the mix between the two strategies (resident or migrant) to be reflected in both geographic and ecological spaces, resulting, at the population level, in intermediate similarity during the migratory season.

Here we describe the study of seasonality of a partially migratory bird, Wood Storks, in both geographic and ecological (specifically climatic) spaces. To facilitate comparison between both spaces, we used a simplified 2-D niche space with two critical climatic components varying throughout the year: temperature and precipitation. We use home range overlap metrics (Fieberg and Kochanny, 2005) to simultaneously investigate similarity of monthly ranges in geographic space and monthly niches in climatic space. Because Wood Storks are a partial migrant breeding in South Florida during winter (dry season) (Coulter et al., 1999), we expect to find high similarity in both spaces during this season, but low similarity during the rest of the year, as a result of a fraction of the population migrating to northern foraging grounds.

2 Material and Methods

2.1 Wood Storks in southeastern U.S.

Sixty-one adult Wood Storks were captured between 2005 and 2011 throughout their southeastern U.S. range in Florida, Georgia, and South Carolina, and equipped with solar-powered Argos/GPS tags. Tagged birds were monitored for an average of 649 ± 563 d from July 2005 to December 2011, and the tags collected a total of 445,638 GPS locations, which is more than 7,000 locations per individual on average ($7,306 \pm 6,036$). We defined the study area by the coastline to the South (i.e. all land masses), and by the limit of a convex hull around all GPS locations to the North (see the study area limits in Fig. 1).

We first grouped all GPS data by month across all years. To account for variability in number of locations among individuals, and the fact that individual Wood Storks are a random sample of the population, we sampled 5,000 GPS locations in each month by 1) removing individuals with fewer than 100 locations in a given month, and 2) sampling 5,000 random individual Wood Storks (with replacement) and 1 random location for each of the 5,000 sampled individuals. We thus compiled with 60,000 random locations for the population, evenly distributed throughout the year.

In climatic space, the Wood Stork niche was described by average monthly temperature and precipitation using climate rasters from the Climate Research Unit (CRU) data set, available at a resolution of approximately 10 arc-min (New et al., 2002). A previous analysis (Watling et al., 2012) showed that variables describing monthly climate (e.g., mean monthly temperature and precipitation) performed equally well as the more ecologically sensible "bioclimate" variables derived from seasonal relationships between precipitation and temperature (e.g. maximum temperature of the warmest month, or mean precipitation of the driest month) to define climatic niches of twelve terrestrial vertebrate species in the southeastern U.S. Remarkably, the only exception were Wood Storks, which can be explained by the global range of the species spanning both hemispheres, hence effectively preventing

monthly variables to be meaningful (Watling et al., 2012). Focusing on the southeastern U.S. range only circumvents this issue, and actually supports the use of monthly variables as the simplest approach.

Global layers were clipped to the study area, and temperature and precipitation at sampled locations defined a 2D-climatic niche, similar to the range defined in the 2D-geographic space (longitude and latitude) by GPS locations. To allow meaningful comparison between temperature/precipitation and longitude/latitude, the former were standardized as to be on the same scale (subtraction of the mean followed by division by the standard deviation for all locations).

2.2 Geographic and climatic similarity

We computed utilization distributions (UDs), i.e. the bivariate probability density associated with Wood Storks in both geographic (defined by longitude and latitude) and climatic (defined by standardized temperature and precipitation) spaces using the kernel method (Worton, 1989) with standard parameterization (*ad-hoc* method for the smoothing parameter, which supposes a bivariate normal UD). We then measured overlap in both geographic and climatic spaces throughout the year with Bhattacharyya's affinity (BA), which defines seasonal similarity Cagnacci et al. (2016). The BA is a synthetic measure (i.e. symmetric) appropriate to quantify the overall similarity of two UDs (Fieberg and Kochanny, 2005), and ranges from zero (no overlap) to 1 (identical UDs).

2.3 Marginality

Different constraints acting in the climatic and geographic spaces render quantitative comparison of overlap in both spaces difficult. Instead, as the geographic range bounds what is available to a species, it is possible to better understand the dynamics at play in climatic space by further investigating monthly habitat selection by means of marginality. Marginality, the vector connecting the centroid of environmental conditions in the geographic area

and the centroid of conditions in the niche, measures the difference between available and used conditions (Hirzel et al., 2002; Basille et al., 2008). In our case, we used marginality to measure the difference between climatic conditions in the study area and climatic conditions at Wood Stork GPS locations as temperature and precipitation change month by month throughout a year. Note here that the study area, in climatic space, is completely defined throughout the year as the union of the 12 monthly climate layers.

3 Results

There was greater consistency in geographical space than in climatic space (Fig. 2), despite large geographic variation during the year (see Appendix A). Overall, similarity (overlap) in the geographic range between any two months was always greater than 50 %, with minima reached between the months of January–February and July–September (consistently between 51–55 %). On the other hand, similarity in the climatic space was much lower, ranging from 0 % between many months throughout the year, to a maximum of 83 % between July and August. In particular, similarity from successive months ranges from 6 % to 83 % (mean±SD: 42.0±23.5) in the climatic space vs. 89 % to 99 % (mean±SD: 94.8±3.4) in the geographic space.

The different patterns of seasonal change in geographic and niche space confound interpretation of the overlap in both spaces. For instance, the use of a 90 % threshold in the geographic space delineates two very consistent seasons, Summer from April to October included, and Winter from November to March included (Fig. 2). However, transitions from each season are very smooth, with high values of overlap (89 %) in both cases. In other words, the evolution of the geographic distribution is very progressive from month to month. Conversely, using thresholds as low as 35 % in the climatic space still delineates two seasons, Summer from June to October included, and Winter from November to February included, which are actually subset of the seasons previously defined in the geographic space (Fig. 2).

Within-season consistency is greater in geographic space than in climatic space: the lowest similarity between any two months for a given season is 84 % (between April and September, and between May and September), while similarity drops to 1 % in the climatic space, even in the subset seasons (between July and October) (Fig. 2). This highlights both the high consistency of monthly ranges as compared to monthly climatic niches, but also the higher discriminatory power of the latter, due to larger contrasts.

Finally, monthly marginality in climatic space (i.e. the average difference between monthly climatic conditions in the study area and climatic conditions used by Wood Storks) highlighted a very clear picture of an annual cycle (Fig. 3): Wood Storks consistently used areas wetter and slightly warmer than generally available in their range during the summer (July–August), and consistently used warmer and drier areas during the winter (November–April). Transitional months between these two seasons appeared clearly to be May and October, with areas used by Wood Storks in these two months warmer and slightly wetter than generally available in their entire range. In fact, marginality in May and October were very similar, and much more similar to each other than to any other month of the year (Fig. 3).

4 Discussion

In this study, we investigated seasonal similarity in both geographic space (range) and ecological space (climatic niche) of the partially migratory Wood Storks in the southeastern U.S. Using home range metrics of overlap, we highlighted seasonal consistency in both spaces: a summer season (wet season: June–September *a minima*) and a winter season (dry season: November–February *a minima*) have been identified in both geographic and climatic spaces, punctuated by intermediate seasons (April–May and October). This resulted in Wood Storks using drier and warmer areas than generally available in the study area during the winter, but wetter areas during the summer. However, more consistent similarity in the geographic than in the climatic space indicated a hierarchy of factors leading to seasonal space use, with

climate alone unable to fully explain temporal patterns.

The lowest value of geographic overlap occurred between the months of January and July/August, and is still greater than most values of climatic overlap. While it might be surprising for a migratory species—one would expect low geographic overlap associated with greater climatic overlap—this can be in part explained by their migratory strategy: Wood Storks are partially migratory (Coulter et al., 1999), which results in some individual migrating while others stay resident year-round. As a consequence, the overall (monthly) distributions at the population level are not as contrasted as would be for a fully migratory species, especially between migration phases. This result is highly similar to Golden Eagle (*Aquila chrysaetos*), which expressed high overlap (BA $= 87 \pm 9$) between breeding and non-breeding home ranges in western U.S. (Watson et al., 2014), but can also be compared with very low values (< 10) of overlap at the individual level for large migratory vertebrates, with minimum overlap as low as 3 (reindeer *Rangifer tarandus*) or 8 (red deer *Cervus elaphus*) documented in Norway (Cagnacci et al., 2016). Despite the very high geographic overlap in our study system, BA (Fieberg and Kochanny, 2005) showed enough fluctuation to define clear seasons in the geographic space as well.

On the other hand, similarity in the climatic space was surprisingly low, and defined narrower seasons. While BA delineated clear seasons in the climatic space, their values were consistently lower than the corresponding ones in the geographic space, indicating higher fidelity in space than for climate—or, in other words, that seasonal ranges are sought after for different features than their climatic characteristics. Over the long term, birds have been shown to somewhat track climate change, however at a slower pace than the actual climatic shift (Devictor et al., 2008). Altogether this seems to indicate that birds' fidelity to specific areas could counteract their need to track climatic conditions at both fine (within year, this study) and large (across years, Devictor et al., 2008) temporal scales. However, and contrary to our expectations, climatic consistency was greater during the wet season than during the dry season, as shown by larger BA values in between June–October than during

the rest of the year. This is potentially a consequence of the low climatic variability during summer throughout the Southeastern U.S.: it is wet and hot everywhere in the range, and despite Wood Storks occupying a larger area, available conditions are narrower than during the winter.

Habitat selection—in terms of temperature and precipitation—was remarkably stable within each season (especially during the summer), even though average climatic conditions still vary greatly from month to month in the study area. This is another indication of geographic constraint: instead of tracking climate conditions directly, Wood Storks settle in specific areas, directly constraining available conditions in a given season. These areas are in turn associated with climatic conditions different than the rest of the range, however still varying in each season. Wood Storks are heavily tied to prey availability, especially during the breeding season, which is directly regulated by local hydrology of the wetland (Kahl, 1964). As a result, Wood Storks are potentially more sensitive to local variations in weather (especially rain) than average monthly climatic conditions (Borkhataria et al., 2012). As Wood Storks are constrained to their nests during the breeding season (generally February–May, Coulter et al., 1999), their winter range corresponds to the driest areas of the year-round distribution, which are associated with the best foraging opportunities (Coulter et al., 1987; Herring and Gawlik, 2011).

Historically, south Florida was host to large breeding populations of wading birds, including Wood Storks, although their number have sharply declined with the drainage of South Florida's wetlands (Frederick and Ogden, 2003). The date of nest initiation has been delayed by several months (February–March vs. historical November–December initiations) in response to deteriorating habitat conditions (Frederick et al., 2009). With sufficient sample size (i.e. enough individuals monitored simultaneously and over several years to bring a good generalization power), our framework could be used to highlight fine-scale dynamics within single years, and investigate temporal trends (e.g. directly related to the timing of migration) over time.

We used a simplified definition of the niche in two dimensions only—arguably, temperature and precipitation are amongst the most critical climatic variables that define niche dynamics (Luoto et al., 2007; Bucklin et al., 2015). However, ecological niches, even restricted to their climatic form, are highly dimensional constructs, and by extension, the ecological space too. Our approach measuring overlap is by no means restricted to a plane. While measures of multi-dimensional overlap exist (see for instance an alternative approach of a multivariate index of niche overlap based on Tukey depth in Cerdeira et al., 2018), it is unclear how the resulting indexes can be compared to a 2-dimensional index of geographic overlap, as overlap mathematically decreases with higher dimensionality. A first step is thus to reduce the ecological space to two dimensions, using multivariate analyses, and focus on the first two axes of the analysis, which typically account for most of the information (see e.g. Dallas et al., 2017). In this particular case of temporally-varying niches, the K-select (Calenge et al., 2005) provides a natural way to find commonalities between monthly climatic niches, which are essentially similar to individual habitat selection with varying availability.

While seasonality can be addressed in both spaces separately (home range dynamics in the geographic space, e.g. Lesage et al. 2000, dynamic habitat use in the ecological space, e.g. Basille et al. 2013), little attention has been devoted to a joint approach (but see Peters et al., 2017). We aimed to fill this gap by providing a simple, yet very general approach to explore seasonal variability in geographic and ecological spaces, which should prove very useful in dynamic ecosystem (La Sorte et al., 2018). For instance, the correspondence between the geographic and the ecological space is at the core of species distribution modeling, which infers potential range maps by considering all suitable areas, and predict future potential ranges under changing conditions, such as climate change (Elith and Leathwick, 2009). While in a stable, saturated system, ecological niches provide a direct equivalence to the geographic range (Soberón and Peterson, 2005), it becomes increasingly critical to account for variation (seasonality, long-term trends) in natural ecosystems.

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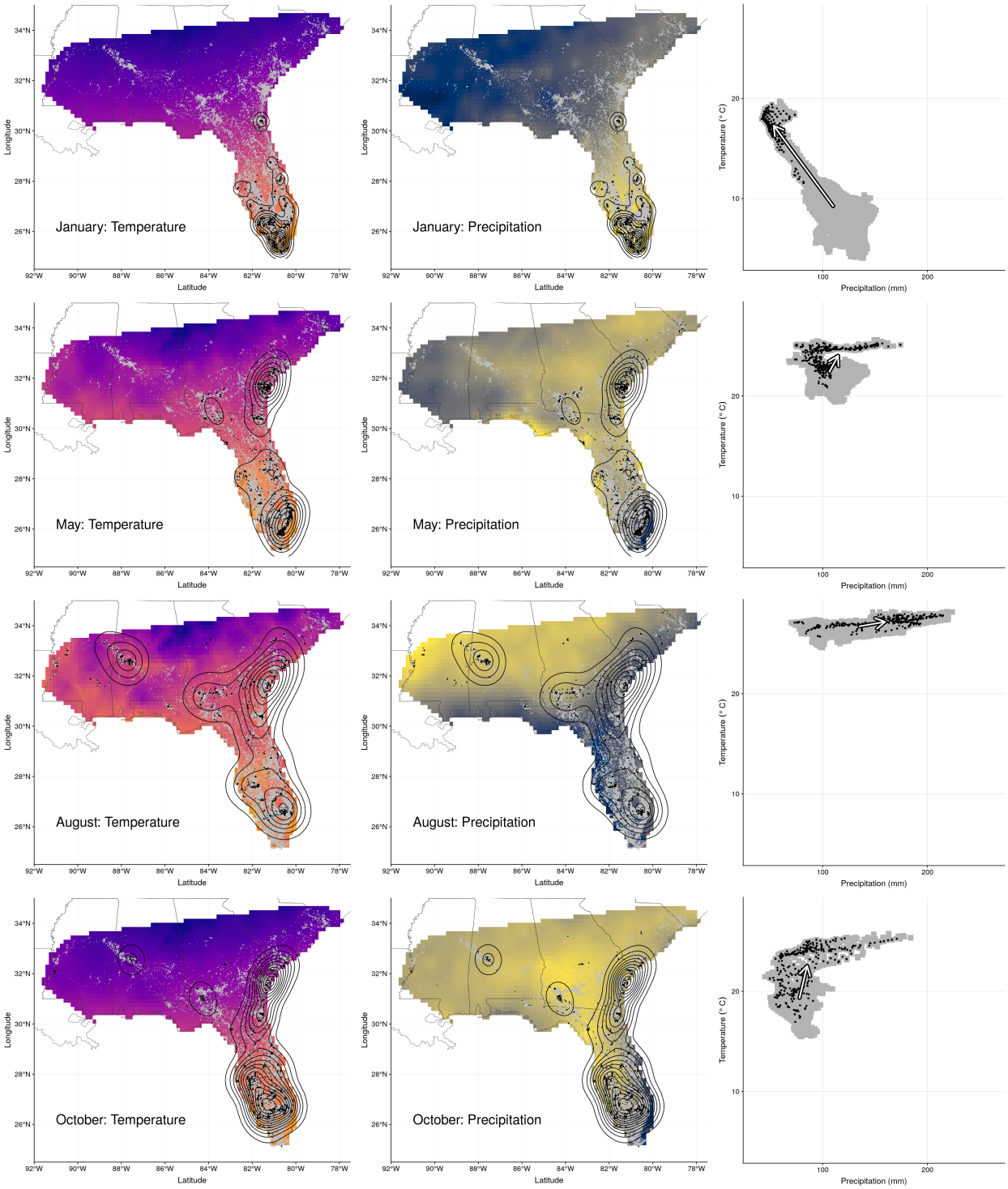
Figures

Figure 1: Evolution of geographic distributions and climatic niche during the year, in January (winter season), May (transition), August (summer season) and October (transition). Each panel presents monthly ranges (left) and climatic niche (right). Range maps show current GPS locations in a given month in black (with kernel contour lines), and all locations from the entire dataset shown as a reference in gray, on a background of temperature (monthly temperatures on a yearly color scale going from blue for colder temperatures to red for warmer temperatures). Climatic niches show current conditions used in a given month (precipitation on the X-axis, and temperature on the Y-axis) in black, in comparison to conditions available in the study area in a given month in gray. The arrow defines marginality in the climatic space, and links average available conditions to average used conditions—the longer the arrow, the more pronounced habitat selection is in that direction.

Figure 2: Matrix of monthly geographic (lower triangle) and climatic (upper triangle) similarity used to delineate consistent seasons throughout the year. The matrix provides Bhattacharyya's affinity as a percentage (between 0 and 100, higher values corresponding to darker color), as a measure of overlap between two months i (rows) and j (columns). The main diagonal, where $i = j$ is grayed out as all values equal 1. Consistent seasons in both spaces are highlighted with a bold line (June–October and November–February), while larger seasons identified in the geographic space only are highlighted with a solid and a dashed line in the geographic and climatic spaces, respectively (April–October and November–March).

Figure 3: Seasonal variation in marginality, as measured by the difference between climatic conditions at Wood Stork GPS locations vs. the entire study area for each month. Each arrow represents selection in a given month for both precipitation (X-axis) and temperature (Y-axis): Wood Storks select drier and warmer areas during the winter (November–April in fuchsia), wetter areas during the summer (June–September in dark blue), and intermediate conditions in transitional seasons (May and October in orange).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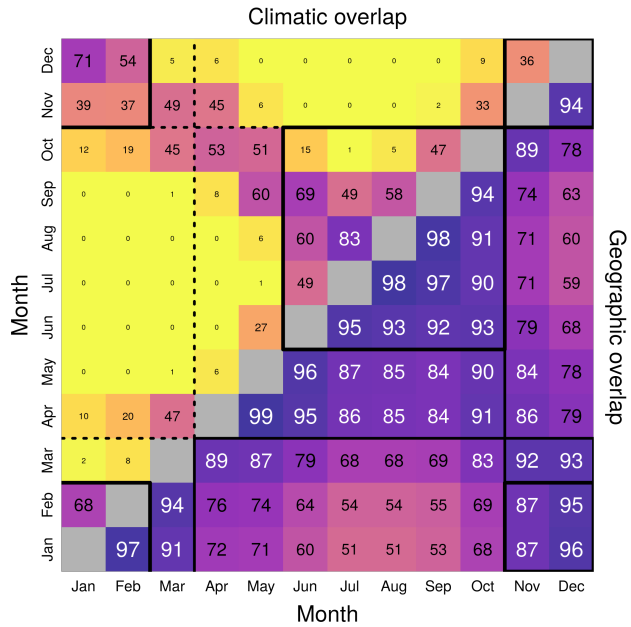
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Aug 0 0 0 0 6 60 83 98 91 71 60
Jul 0 0 0 0 1 49 98 97 90 71 59
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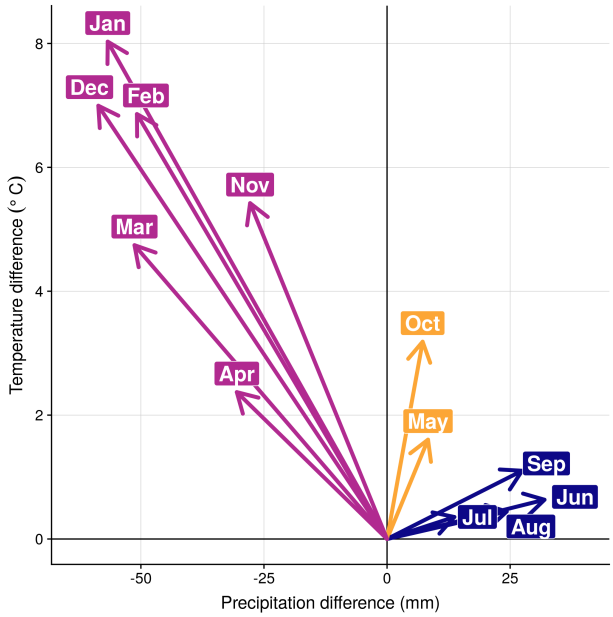
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Sep
Jun
Jul
Aug
8
6
4
2
0
-50
-25
0
25
Temperature difference (° C)
Precipitation difference (mm)

A Wood Stork monthly ranges and climatic niches

An animation of Fig. 1 presenting all 12 monthly ranges and climatic niches is available at: https://mablab.org/wood-storks/clim-niche/

In the animation, each panel presents monthly ranges (left) and climatic niche (right). Range maps show current GPS locations in a given month in black (with kernel contour lines), and all locations from the entire dataset shown as a reference in gray, on a background of temperature (monthly temperatures on a yearly color scale going from blue for colder temperatures to red for warmer temperatures). Climatic niches show current conditions used in a given month (precipitation on the X-axis, and temperature on the Y-axis) in black, in comparison to conditions available in the study area in a given month in dark gray. The arrow defines marginality in the climatic space, and links average available conditions to average used conditions—the longer the arrow, the more pronounced habitat selection is in that direction. Combined yearly conditions are presented in the background in light gray to provide a stable reference throughout the year.