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Further perspectives on the breeding distribution of migratory birds: South American austral migrant flycatchers

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Summary

1. Patterns of distribution of breeding austral migrant tyrant-flycatchers in temperate South America were quantified and analysed in conjunction with a variety of ecological, biogeographical and climatic variables.
2. The pattern of proportion of migratory to total breeding tyrannids was most strongly associated with latitude and two temperature variables, mean temperature of the coldest month and relative annual range of temperature.
3. The strong associations of latitude and temperature with percentage of migrants are consistent with the results of most similar investigations of the breeding distributions of migratory birds, both for migrants breeding in North America and in Europe, but contradict the hypothesis that habitat complexity plays a major role in structuring the proportion of migrants in communities of breeding birds.
4. The consistency of results among studies of migrants on different continents suggests that temperature and latitude, presumably a surrogate for one or more climatic variables, are globally significant factors in the breeding distributions of migratory birds.
5. The results for austral migrant flycatchers are consistent with the hypothesis that the prevalence of migration at any particular locality is ultimately dependent on the abundance of resources in the breeding season and the severity of the winter season, or on the difference in resource levels between summer and winter.

Key-words: bird migration, climate, geographical range, latitude, temperature.

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Introduction

Migration is a behaviour that allows exploitation of seasonally productive environments. Because local environments differ in their capacity to support migratory birds, the proportion of migratory to resident birds is geographically variable. Patterns in the distribution of migratory birds are thus evident at continental and global scales, and afford opportunities for the investigation of geographical trends in migratory tendency and environmental and biotic factors associated with these trends. Accurate distributional information has been most readily available for portions of the north temperate zone, so studies of geographical trends in migration have historically been concentrated on the breeding grounds of North American and European migrants.

MacArthur (1959), for example, studied the proportion of migrants breeding in a number of communities in temperate North America. He concluded that the percentage of migrants was relatively uniform within habitat types, and that habitat complexity determined degree of seasonality and thus the percentage of migrants at a locality, with more complex habitats supporting the highest percentages of migrants. He also argued that there was no simple correlation between percentage of migrants and climate, or percentage of migrants and latitude.

Willson (1976) re-examined the distributional patterns of North American migrants and suggested, *contra* MacArthur, that the pattern of distribution of migratory birds in North America had a strong latitudinal component. She proposed that latitude acted through one or more climatic variables to produce

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the pattern of distribution of migrant birds in North America. Although she did not test the idea, she also predicted that the influence of climatic variables should be evident within habitat types, resulting in within-habitat variability, rather than the relative uniformity of within-habitat percentages reported by MacArthur.

Herrera (1978) quantitatively analysed patterns of the breeding distribution of migrants in European bird communities and likewise found a strong latitudinal component to the pattern. He found that percentage of migrants was most strongly influenced by latitude and that the primary determinant of this pattern was average temperature of the coldest month. This pattern was supported when single habitat types were examined, in accordance with Willson's prediction for North American migrants.

More recently, Newton & Dale (1996a) adopted a different approach to the study of distributional patterns of western European migratory birds. They used distributional information to calculate percentage of migratory species breeding at successive 5° lines of latitude, rather than at particular localities, and then attempted to account for the observed patterns using environmental variables, as well as latitude. They found that latitude showed the strongest associations with percentage of breeding migrants, and that mean annual temperature showed the second strongest relationship. A similar study (Newton & Dale 1996b) was conducted on migrant birds in eastern North America, with similar conclusions.

Although the most well-known migratory birds are those that breed in North America and Europe, migratory birds also breed in the Southern Hemisphere. The most extensive of the southern migration systems is the austral, or southern, system of South America (Chesser 1994); austral migrants are bird species that breed in south temperate South America and migrate north, towards or into tropical South America, for the southern winter. Austral migration represents a third temperate–tropical migration system, in the sense that the term has been applied to the Northern Hemisphere systems, and provides an opportunity for further investigation of the breeding distributions of migratory birds and the processes underlying these distributions. This paper discusses patterns of breeding distribution of the major group of austral migrant birds, the tyrant-flycatchers, across temperate South America, and the relative importance of environmental factors associated with these distributional patterns.

Materials and methods

Methodology for studying the breeding distributions of migrant birds has varied considerably, in terms of taxonomic portion of the avifauna investigated, types of migratory birds included, whether distributional or census data were used, and whether migratory species or individuals were used as the unit of analysis. MacArthur (1959) analysed census results for passerine and non-passerine landbirds, and considered as migratory only those species that winter primarily in the Neotropics. Willson (1976) also analysed censuses of both passerine and non-passerine landbirds, but considered, in addition to Neotropical migrants, *any* species that vacates a breeding locality in winter. Herrera (1978), in contrast, analysed only passerine birds, and, like MacArthur, considered as migratory only those species that winter in the tropics. Newton & Dale (1996a, b) based their research on distributional data and considered all bird species in their analyses. Herrera (1978) and Newton & Dale (1996a, b) examined patterns of total numbers, as well as percentages, of migrants, whereas MacArthur (1959) and Willson (1976) both concentrated on percentages. MacArthur, Willson and Herrera each concentrated on analysis of percentage of migratory individuals at each locality, although MacArthur and Willson also provided data on percentages of migratory species, whereas Newton and Dale considered data on migratory species only.

This study quantifies the relationship between migratory tendency of tyrant-flycatchers at particular localities and a number of environmental variables, with the following conventions. First, because detailed census data are not available for South American birds, it was necessary to analyse data on migratory species only, as derived from distributional data. Second, because detailed seasonal distributional information is available only for austral migrant tyrant-flycatchers, analyses have been restricted to members of the family Tyrannidae. Tyrant-flycatchers are the predominant group of austral migrants, the 74 migratory species constituting more than 50% of passerine austral migrant species. Their suitability is enhanced by their ecological, behavioural and morphological similarity to members of a variety of taxonomic groups in other migration systems; for example, ecological and behavioural overlap is extensive between austral migrant flycatchers and the migrants (predominantly from the families Muscicapidae, Sylviidae, Turdidae and Laniidae) in Herrera's (1978) study of the breeding distribution of European birds. Third, this study considered as migratory any species that vacates its breeding locality in winter, including many that are permanently resident in other portions of their ranges (cf. Newton & Dale 1996a, b). As Willson (1976) noted, all species that vacate breeding grounds in winter presumably do so because of declining resource availability or other aspects of seasonality, and there is no compelling reason for excluding any of them based on location of their wintering grounds.

Distributional information for resident flycatchers was based on the maps in Ridgely & Tudor (1994). Because of inaccuracies concerning distributions of austral migrants embedded in the ornithological literature (see Marantz & Remsen 1991; Chesser &

Marín 1994), distributional data for migratory flycatchers were based on a re-analysis of the seasonal and geographical distribution of each species, including a thorough evaluation of all available specimen records and published observational data (Chesser 1995). Patterns of seasonal distribution were determined by data on the presence and absence of species; the extensive geographical and temporal coverage afforded by year-round collecting and observational activity in temperate South America provided for accurate determination of patterns of seasonal distribution for the areas used in this study. Species were considered to breed at a locality if: (i) the locality lies within the summer-resident or permanent-resident range of the species; and (ii) the elevational and ecological conditions at the locality are appropriate for the species. Proportion of migrants (PM) was calculated as number of species of summer-resident (= migrant) tyrant-flycatchers at each locality divided by number of species of summer-resident plus permanent-resident tyrant-flycatchers at that locality. For purposes of comparison with previous studies, species occurring solely in winter were not included in the analyses; numbers of winter residents in the south temperate zone were small relative to numbers of summer and permanent residents. Climatic information was taken from the most recent available volume of the World Weather Records series (National Oceanic & Atmospheric Administration 1982). The 28 localities used in the analysis are a subset of those for which climatic data were available, and were selected to be representative of geographical, elevational, habitat and climatic diversity, to the extent that this was possible (Table 1, Fig. 1). For one locality, missing precipitation information was interpolated from a climatic atlas (World Meteorological Organization 1975).

Ecological, biogeographical and climatic variables analysed for each locality were: (i) total number of flycatcher species, including migrants plus residents; (ii) 'structural complexity' of the predominant natural vegetation at that locality (HAB), based on the vegetational map of Hueck & Seibert (1972), ranging from 1 to 5 [1 = desert or puna, 2 = steppe or pampa, 3 = scrub, 4 = woodland, 5 = forest; habitat quality of two localities within the pampa zone but situated adjacent to riverine woodlands was designated as 3 (average of 2 and 4)]; (iii) latitude (LAT), in degrees and hundredths of degrees; (iv) elevation above sea level (ELEV), in metres; (v) shortest distance in km to the nearest open ocean (DISC); (vi) shortest distance in km to the open Pacific Ocean (DISP); (vii) mean annual temperature in °C (MAT); (viii) mean monthly temperature in °C of the coldest month (CM); (ix) mean monthly temperature of the hottest month (HM); (x) absolute yearly range in temperature (ART) in °C, obtained by subtracting CM from HM; (xi) relative yearly range in temperature (RRT), obtained by dividing ART by HM; (xii) mean annual precipitation in mm (MAP); (xiii) mean monthly precipitation of the driest month in mm (DM); (xiv) mean monthly precipitation of the wettest month in mm (WM); (xv) absolute yearly range in precipitation (ARP), obtained by subtracting DM from WM; and (xvi) relative yearly range in precipitation (RRP), obtained by dividing ARP by WM.

Relative importance of factors associated with the breeding distribution of austral migrant flycatchers was investigated using simple linear and quadratic regression analyses and stepwise regression analysis. Simple regression analyses were performed to establish the general association between migration and the 16 environmental variables; linear and quadratic regressions were used to determine the fit of the associations to both lines and curves. Separate simple regression analyses were conducted using each environmental variable as the independent variable, with PM as the dependent variable, using both linear and quadratic functions. Stepwise regression analyses were conducted because of the correlations among the environmental variables (see Appendix). Stepwise regression analyses were conducted on standardized data with PM as the dependent variable and the environmental variables as independent variables; the F-value to enter the equation was set at 4·0, and F to remove at 3·996. Both simple and stepwise regressions were performed using Statview II (Abacus Concepts Inc., Berkeley, CA, USA).

Results

The percentage of migratory flycatchers in temperate South America ranges from 100% in southernmost South America to roughly 20% in parts of south-eastern Brazil (Fig. 1, Table 1). The simple linear regression analyses indicated that latitude was the single variable most closely associated with percentage of migrant species ($r^2 = 0{\cdot}82$; Table 2). The relationship was positive, indicating that an increase in the latitude of a locality was associated with an increase in the percentage of migrants at that locality. Regressions of percentage of migrants (PM) against latitude within all habitat types were also significant (Table 3).

The climatic variable most closely associated with percentage of migrants, and the one with the second strongest relationship overall, was mean temperature of the coldest month (CM; $r^2 = 0{\cdot}74$), which was negatively associated with PM (Table 2). Other variables with highly significant associations were total number of species ($r^2 = 0{\cdot}61$, negative association), mean annual temperature ($r^2 = 0{\cdot}61$, negative), distance from the Pacific ($r^2 = 0{\cdot}45$, negative), mean temperature of the hottest month ($r^2 = 0{\cdot}40$, negative), and relative range of temperature ($r^2 = 0{\cdot}33$, positive).

Results of the stepwise regression analysis, because it was also linear, indicated that latitude was again the single variable explaining the largest amount of variation in percentage of migratory species

Table 1. List of the 28 temperate South American localities used in this study, with geographical coordinates (degrees and minutes south latitude/degrees and minutes west longitude), elevation, habitat score, total number of migratory flycatcher species, and percentage of flycatcher species that migrate

Locality	Lat./long.	Elevation (m)	Habitat	Migrants (*n*)	Migrants (%)
Londrina, Braz.	2323/5111	560	5	14	23·3
Concepción, Par.	2325/5715	70	3	19	38·0
São Paulo, Braz.	2330/4637	790	5	13	17·1
Salta, Arg.	2451/6529	1220	4	17	48·6
Las Lomitas, Arg.	2442/6035	130	3	12	35·3
Curitiba, Braz.	2526/4916	910	5	17	25·4
Villa Rica, Par.	2545/5626	150	5	23	34·3
Tucumán, Arg.	2650/6512	410	4	25	47·2
Corrientes, Arg.	2727/5846	60	5	18	38·3
La Rioja, Arg.	2923/6649	420	4	11	52·4
La Serena, Ch.	2954/7115	160	2	2	33·3
Porto Alegre, Braz.	3002/5113	10	3	13	35·1
Pilar, Arg.	3140/6353	330	3	19	59·4
Cristo Redentor, Arg.	3250/7005	3810	1	4	80·0
Rosario, Arg.	3255/6047	20	3	16	55·2
Treinta y Tres, Ur.	3311/5421	50	2	14	50·0
San Luis, Arg.	3316/6621	710	4	17	68·0
Buenos Aires, Arg.	3435/5829	20	3	19	57·6
Constitución, Ch.	3519/7225	10	3	4	44·4
Santa Rosa, Arg.	3635/6416	180	3	17	73·9
Bahia Blanca, Arg.	3844/6211	80	3	12	57·1
Bariloche, Arg.	4109/7110	830	4	12	70·6
Maquinchao, Arg.	4115/6844	880	2	12	85·7
Trelew, Arg.	4314/6518	30	3	10	76·9
Puerto Aysén, Ch.	4524/7242	10	5	5	83·3
Puerto Deseado, Arg.	4744/6555	70	2	9	90·0
Río Gallegos, Arg.	5137/6917	10	2	4	100·0
Ushuaia, Arg.	5448/6819	1	5	7	100·0

($r^2 = 0{\cdot}82$; Table 4); CM explained the largest amount of variation when latitude was excluded from the analysis ($r^2 = 0{\cdot}74$; Table 5). Relative range of temperature (RRT) explained the second largest amount of variance in the stepwise analysis and was positively associated with PM, given the effect of latitude (total $r^2 = 0{\cdot}89$; Table 4). Thus, percentage of migrants increased with RRT over and above the increase associated with latitude. Absolute range of temperature (ART) explained the third largest amount of variance and was also positively associated with PM, given the effects of the first two variables (total $r^2 = 0{\cdot}94$); therefore, having accounted for latitude and RRT, percentage of migrants increased with ART. The final three variables in the regression equation, explaining the fourth, fifth, and sixth largest amounts of variance, were distance from the coast, mean temperature of the coldest month (CM), and mean annual temperature (MAT). Thus, four of the five temperature variables entered the regression equation, although RRT and ART were later removed, following the addition of CM and MAT, respectively.

Results of the quadratic regressions were similar in most cases to the linear ones, but revealed two differences (Table 2). Relative range of temperature (RRT) became the variable most closely associated with percentage of migrants in the quadratic analyses ($r^2 = 0{\cdot}92$), surpassing latitude, and mean temperature of the wettest month also showed a much stronger relationship than in the linear regressions ($r^2 = 0{\cdot}50$). The relationship between RRT and percentage of migrants was positive; thus, an increase in relative range of temperature at a locality was associated with an increase in percentage of migrants.

Discussion

The primary environmental factors associated with percentage of migratory flycatcher species across temperate South America were latitude and temperature, which are themselves related to some extent. Increases in percentage of migratory flycatchers per locality were most closely associated with increasing latitude in the linear analyses, and secondarily with declining winter temperatures and increasing relative range of temperature. In the quadratic analyses, percentage of breeding migrants per locality was most strongly related to relative range of temperature, and secondarily to latitude. Non-temperature variables significantly but less strongly associated with percentage of migrants included distance from the nearest coast. Variables weakly associated with percentage of species of migratory flycatchers included elevation and habitat complexity (*contra* MacArthur 1959). Associations between precipitation and migration were, in general,

Fig. 1. Geographical pattern of proportion of tyrant-flycatchers migratory at 28 temperate South American localities.

Table 2. Results of simple linear and quadratic regressions of various ecological, biogeographical and climatic variables on percentage of migrant species of tyrant-flycatchers at localities in temperate South America. Probability values are: $^{*}P < 0{\cdot}05$, $^{**}P < 0{\cdot}01$, $^{***}P < 0{\cdot}001$

	Linear		Quadratic
	slope	r^2	r^2
No. spp.	–	0·61***	0·61***
Habitat	–	0·12	0·14
Latitude	+	0·82***	0·82***
Elev.	+	0·01	0·09
Dist. coast	–	0·11	0·12
Dist. Pacif.	–	0·45***	0·47***
MAT	–	0·61***	0·61***
CM	–	0·74***	0·77***
HM	–	0·40***	0·40***
ART	+	0·20*	0·22*
RRT	+	0·33**	0·92***
MAP	–	0·14*	0·48***
DM	–	0·00	0·17
WM	–	0·19*	0·50***
ARP	–	0·32**	0·41**
RRP	–	0·18*	0·20

much weaker than those between temperature and migration.

Table 3. Results of regressions of percentage of migrant species within habitat types against latitude for austral migrant flycatchers at 28 localities in temperature South America. Habitat types 1 and 2 were combined because there were only two localities of type 1. P-values are: $^{*}P < 0{\cdot}05$, $^{**}P < 0{\cdot}01$, $^{***}P < 0{\cdot}001$

Habitat type	n	r^2 (vs. latitude)
1+2	6	0·71*
3	10	0·66**
4	6	0·73*
5	6	0·98***

It should be noted that these analyses suffer to a degree from the statistical problem that occurs in any geographical study of this type, that of non-independence; for example, although many pairs of the 28 localities share no species, many other localities do have species in common. The problem of non-independence, however, is mitigated by the strength and clarity of the results, which typically explain some 80% of the variation in any analysis. Although the statistics used in most of the analyses claim 27 degrees of freedom, the correlation between latitude and PM, for instance, is strong enough that it would be sig-

Table 4. Results of stepwise regression analyses, using standardized data. The dependent variable is percentage of flycatcher species migratory at a locality. Independent variables are 16 ecological, climatic and geographical variables (see text). (*variable removed from equation following entry of mean temperature of coldest month; **variable removed following entry of mean annual temperature)

Independent variables	Order entered	Total r^2	*F*-value
Latitude	1	0·82	114·68
Relative range temp.*	2	0·89	102·58
Absolute range temp.**	3	0·94	132·08
Distance from nearest coast	4	0·96	143·98
Mean temp. of coldest month	5	0·97	142·85
Mean annual temp.	6	0·98	211·57

Table 5. Results of stepwise regression analysis of percentage migratory flycatcher species, with latitude excluded. Independent variables are 16 ecological, climatic and geographical variables (see text)

Independent variables	Order entered	Total r^2	*F*-value
Mean temp. of coldest month	1	0·74	73·97
Elevation	2	0·87	85·88
Distance from nearest coast	3	0·93	108·74
Mean annual temp.	4	0·95	103·10
Relative range of precip.	5	0·96	112·58
Relative range of temp.	6	0·97	109·75

nificant for as few as 3 d.f., far below the actual value; the strength of other results is similar in this respect.

The associations of percentage of South American austral migrant flycatchers with latitude and temperature are consistent with the results of Willson (1976) and Newton & Dale (1996b) for North American migrants and of Herrera (1978) and Newton & Dale (1996a) for migrants in Europe, all of whom stressed the importance of latitude and climatic variables, especially temperature. The consistency of results, in spite of differences in methodology among studies on different continents, indicates the relative robustness of these associations and suggests that globally significant processes influencing the distributional patterns of migratory birds have been identified.

The results of this study are strikingly similar to those of Herrera (1978) for European migrants. Herrera's stepwise regression analyses indicated, as did those in this study, that percentage of migratory passerines in European bird communities was most strongly associated with latitude, and that the primary climatic variable associated with this pattern was mean temperature of the coldest month. My results for within-habitat variability in percentage of migrants are likewise similar to those of Herrera, and are consistent with the predictions of Willson (1976). Percentage of migratory flycatchers within habitat types was highly variable, and within-habitat regressions of latitude were significant for all habitat types.

Although both Herrera (1978) and Newton & Dale (1996a, b) found latitude to be most strongly associated with percentage of migrants in Europe and North America, both acknowledged that latitude *per se* was unlikely to have been the ultimate cause of the distributional patterns they observed, and that it was probably a surrogate for one or more climatic factors. The results for South American austral migrant flycatchers, as well as those for European and North American migrants, suggest that temperature is the climatic factor most likely to influence the distributions of breeding migratory birds, but it is unclear whether temperature itself is the sole important variable, or whether an amalgamation of variables, among which temperature is very important, *together* better explain the observed patterns. Variables other than those considered here or in other studies might include daylength, which is essentially a function of latitude, or length of growing season (Willson 1976).

Because latitude and temperature tend to be closely related, it is difficult to tease apart the confounding influences of these two variables. Newton & Dale's (1996a, b) studies from Europe and North America provided a partial decoupling of these two variables, and suggested that temperature may be of primary importance. They found an average of 17% more migrants by percentage at latitudes in North America than at the same latitudes in Europe, in keeping with the colder North American winter temperatures characteristic of the same latitude (Newton & Dale 1996b). Improved elevational dispersion of sampling sites in studies of percentages of migrants at individual localities [such as this study or that of Herrera (1978)] would also result in a partial decoupling of latitude and temperature, and might provide further resolution of factors associated with the patterns of distribution of migratory birds.

Based on his findings of strong associations between percentage of migrants and both latitude and mean temperature of the coldest month, Herrera (1978) proposed that the prevalence of migration at any particular locality depended on the abundance of resources in the breeding season and the severity of the winter season. The results of Newton & Dale (1996a) were consistent with this hypothesis, as were the results of the present study from South America.

Whether the effects of winter cold are direct or indirect, however, is a matter of some contention. Implicit or explicit in many previous discussions of the distribution of migratory birds (MacArthur 1959; Herrera 1978; Newton & Dale 1996a, b) is the idea that the magnitude of the difference between winter and summer food supply determines these patterns of distribution, and that birds migrate in winter because of decreases in the availability of food. Newton & Dale (1996b) proposed, for instance, that geographical variation in the prevalence of migration is almost certainly caused by variation in seasonal differences in food availability, or the degree to which severe winters annually diminish the abundant summer food supply. Herrera's (1978) model is also based on reductions in winter food supply as the ultimate factor inducing migrant birds to leave the temperate zone.

In a similar vein, Root (1988a) found a link between cold temperatures and the winter distributional patterns of North American birds. She determined that the northern winter distributional boundaries of 60% of North American passerines were associated with average minimum January temperatures, but argued (Root 1988b) that this pattern resulted from physiological limits imposed by cold temperatures, rather than decreases in food availability. Under this view, many temperate-zone migrants must leave their breeding grounds in winter because of physiological stress, independent of resource availability. Root's conclusions were based primarily on a significant correlation between the basal metabolic rates of passerines and their metabolic rates at the northern boundaries of their winter ranges, which was taken to imply that winter ranges are limited by the physiological demands of cold winter temperatures. Thermoregulatory parameters were therefore viewed as determinants of northern winter range boundaries. However, an alternative explanation of these data is that food availability is the primary determinant of northern winter range boundaries, and that thermoregulatory parameters are adapted to climate (Yarbrough 1971; Weathers 1979), in this instance to climate associated with winter range. Indeed, winter diet has been shown to be related to degree of migration in European passerines (Newton 1995), and winter ranges of several North American species have shifted northward coincident with an increase in winter bird-feeding (Tramer 1974). Nevertheless, food availability and physiological stress are not entirely independent of one another, and range boundaries are probably affected by interactions among various biotic and abiotic factors (see also Repasky 1991).

Although temperature variables were strongly associated with proportion of migrants in both this study of South American flycatchers and the most methodologically similar of the previous studies, Herrera's (1978) study of European migrants, the association between CM and percentage of migrants, the strongest among climatic variables in both studies, was much greater in this study ($r^2 = 0{\cdot}74$) than in that of Herrera ($r^2 = 0{\cdot}46$). It is unclear whether this difference can be attributed to real differences between continents or to differences in methodology, such as differing standards for inclusion of migratory species, or the concentration of this study on the highly migratory portion of the South American avifauna and consequent exclusion of certain ecological types (especially seed-eaters). A quantitative re-evaluation of the North American pattern (R.T. Chesser, unpublished information) seeks to clarify these and other aspects of the distributional patterns of migratory birds.

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Appendix

Correlation matrix (values of *r*) for 16 ecological, climatic and biogeographical variables, *P*-values are: $^*P < 0{\cdot}05$, $^{**}P < 0{\cdot}01$, $^{***}P < 0{\cdot}001$.

	Spp. (*n*)	HAB	LAT	ELEV	DISC	DISP	MAT	CM	HM	ART	RRT	MAP	DM	WM	ARP
Spp. (*n*)															
HAB	0·57**														
LAT	−0·76***	−0·23													
ELEV	−0·05	−0·22	−0·18												
DISC	0·42*	0·18	−0·55**	−0·06											
DISP	0·83***	0·33	−0·56**	−0·14	0·11										
MAT	0·75***	0·35	−0·78***	−0·41*	0·64***	0·63***									
CM	0·78***	0·43*	−0·76***	−0·47*	0·53**	0·68***	0·96***								
HM	0·63***	0·27	−0·66***	−0·48**	0·62***	0·54**	0·96***	0·87***							
ART	−0·29	−0·31	0·21	−0·02	0·18	−0·26	0·01	−0·25	0·26						
RRT	−0·51**	−0·49*	0·35	0·80***	0·24	−0·45*	−0·73***	−0·82***	−0·71***	0·19					
MAP	0·49**	0·62***	−0·28	−0·23	0·19	0·44*	0·35	0·44*	0·26	−0·35	−0·37				
DM	0·15	0·40*	0·07	−0·24	−0·07	0·25	0·04	0·13	0·00	−0·25	−0·16	0·89***			
WM	0·51**	0·66***	−0·38*	0·08	0·17	0·37	0·32	0·41*	0·21	−0·39*	−0·32	0·94***	0·73***		
ARP	0·59***	0·65***	−0·54**	0·03	0·27	0·35	0·41*	0·47*	0·28	−0·38*	−0·33	0·75***	0·39**	0·92***	
RRP	0·14	0·01	−0·54**	0·28	0·28	−0·14	0·26	0·22	0·21	−0·01	−0·02	−0·21	−0·53**	0·06	0·38*