Chapter 1

OSTRICH 2011, 82(3): 175–183
Printed in South Africa — All rights reserved

Copyright © NISC (Pty) Ltd
OSTRICH
ISSN 0030–6525 EISSN 1727–947X
doi: 10.2989/00306525.2011.607863

Geographic variation in avian clutch size and nest predation risk along a productivity gradient in South Africa

David Hořák[1]*, Ondřej Sedláček[1], Anna Tószögyová[1], Tomáš Albrecht[2,3], Michal Ferenc[1], Václav Jelínek[1] and David Storch[1,4]

[1] Department of Ecology, Faculty of Science, Charles University in Prague, Viničná 7, CZ-128 44 Praha 2, Czech Republic
[2] Department of Zoology, Faculty of Science, Charles University in Prague, Viničná 7, CZ-128 44 Praha 2, Czech Republic
[3] Department of Avian Ecology, Institute of Vertebrate Biology, Academy of Sciences of the Czech Republic v.v.i, větná 8, CZ-603 65 Brno, Czech Republic
[4] Center for Theoretical Study, Charles University and the Academy of Sciences of the Czech Republic, Jilská 1, CZ-110 00 Praha 1, Czech Republic
* Correspondending author, e-mail: david@natur.cuni.cz

Geographic variation in avian clutch size is thought to be related to the variation in nest predation rate and food availability. We studied predation on artificial ground nests along a large-scale geographic gradient in South Africa characterised by increasing productivity from the deserts in the west to humid savannas in the east, and calculated mean clutch sizes of birds occurring in atlas quadrates surrounding our study sites. Clutch sizes generally increased with increasing productivity and seasonality. The least productive desert site was characterised also by the highest predation rate, whereas all the other sites located in savannas revealed much lower and more or less constant predation rate. We found no evidence for relationship between nest predation rates and clutch sizes of ground-nesting birds. This indicates that food availability is the major factor responsible for geographical variation in bird clutch sizes across South Africa, though high predation rate might also contribute to low clutch size in least productive arid environments.

Introduction

Avian clutch size is believed to be primarily determined by two factors: nest predation and food availability. Nest predation is a major cause of reproductive failure in birds (Ricklefs 1969, Skutch 1985), and therefore represents a strong selective power on the evolution of avian life histories (Martin 1995). To be specific, lower clutch size is thought to have evolved in response to greater predation risk, as it reduces nest exposure time and fitness costs of nest losses (Slagsvold 1982, Skutch 1985). Smaller broods also require fewer visits by parents that may reveal nest location to predators (Skutch 1949, 1985). The second general factor that explains the clutch size variation is food availability. According to Lack (1947) the number of eggs within a clutch corresponds to the number of young which the parents can nourish, i.e. to the actual amount of food during the breeding season. Thus, larger clutch size is expected when higher amount of food is available. Later on, the hypothesis of resource availability was modified by Ashmole (1963) who incorporated population densities. He suggested that population sizes are controlled during the periods when food is scarce, and clutch size is determined by food availability during breeding season relative to population density. For that reason, high seasonality of resources leads to large clutch sizes.

Avian clutch sizes show remarkable geographical variation. The most striking pattern is the decline in clutch size from northern regions to the tropics (Jetz et al. 2008). It is assumed that corresponding variation in nest predation rate (Skutch 1949) and/or availability of food resources lies behind the spatial variation in clutch size (Ashmole 1963, Ricklefs 1980). It has been shown that nest predation differs among habitats and consistent differences can favour evolution of contrasting life history traits (Martin 1993a). Hence, variation in nest predation among environments and along environmental gradients has attracted much scientific attention. A considerable number of studies have dealt with differential predation rates at small spatial scales. Differences in nest predation rate are commonly tested between edge and interior habitats (Lahti 2001, Batáry and Báldi 2004, Spanhove et al. 2009), but there has also been some focus on environmental gradients such as the gradient of urbanization (e.g. López-Flores et al. 2009) or wetland gradients (e.g. Albrecht et al. 2006).

Analogous studies over larger geographical scales, however, are much less frequent and often have lead to conflicting results. Martin (1995), for example, found no significant relationship between latitude and nest predation rate in a set of 123 North American passerines, while the results of Kulesza (1990) on New World passerines do suggest such an effect. Most recently, McKinnon et al. (2010) showed a clear decline in predation risk along a 3 350 km long south–north gradient in the Arctic region of North America.

Large-scale studies offer a unique opportunity to investigate the effects of variation in food availability because several correlates of food resources such as humidity, average annual temperature, or seasonality change dramatically over large geographical scales. Although the causality of relationships in correlative studies is often hard to reveal, examination of relations between predation rate, food availability and avian clutch size can be still informative as the directions of possible relationships between the factors determining clutch size evolution seems to be relatively clear. Environmental characteristics may influence both predation rate (e.g. via habitat structure) and clutch size (via food available to birds). Predation rate may subsequently limit clutch size. Variation in environmental conditions over large spatial scales may thus influence avian clutch sizes directly via food availability and/or indirectly via nest predation rate. It follows that, although it may be difficult to distinguish among mechanisms operating behind geographical variation in clutch size, simultaneous investigations of variation in nest predation rate and clutch size over large-scale environmental gradients and subsequent comparison of several such gradients might bring interesting insights into evolution of clutch size in birds.

Here we describe changes in the rate of artificial nest predation among study sites situated along a long geographical productivity gradient, and compare this with large-scale geographic trends in clutch size. For this purpose, we chose a c. 1 550 km long environmental gradient across South Africa, which has several advantages: (1) it is wide enough to cover areas with extremely low environmental productivity and areas with high productivity, (2) changes in productivity are relatively gradual across South Africa, and (3) although the gradient covers a wide range of environments, it is rather longitudinal and thus situated within one biogeographical unit (the whole area is occupied by relatively similar bird taxa). The general aim of the present study is to describe relationships among estimates of food availability (environmental productivity), nest predation risk (artificial nest predation) and avian clutch size over large spatial scale.

Material and methods

The field work was carried out during November and December 2009 (during the breeding season of birds) at five study sites situated along a gradient of environmental productivity in South Africa (Table 1). Various environments along the transect host considerable number of ground nesting bird species belonging to guineafowls (Numididae), francolins (Phasianidae), bustards (Otididae) and also passerines, especially larks (Alaudidae). Similarly rich communities of potential predators of avian nests occurred at the study sites. Ground nests can be predated by: (1) mammals – including black-backed jackal *Canis mesomelas*, Cape fox *Vulpes chama*, honey badger *Mellivora capensis*, bat-eared fox *Otocyon megalotis*, small spotted genet *Genetta genetta* or yellow mongoose *Cynictis penicillata*; (2) birds – especially crows such as Pied Crow *Corvus albus* or Black Crow *C. capensis*; and (3) snakes – which even include specialists on avian eggs (rhombic egg-eater *Dasypeltis scabra*). Field work proceeded according to the breeding season of birds at each study site, starting in the west (Pofadder) and finishing in the east (Punda Maria; Table 1). For each study site, we obtained the normalised difference vegetation index (hereafter NDVI), an estimate of environmental productivity based on the spectral properties of vegetation (the average NDVI estimates in January and July—in these months the highest differences in NDVI distribution are observed—were obtained from ARTEMIS; Africa Real Time Environmental Monitoring Information System, Food and Agriculture Organization of the United Nations, http://www.fao.org/geonetwork/srv/en/). We also calculated seasonality in NDVI as the difference between NDVI estimates in January and July. Furthermore, we measured relative vegetation cover for 32 plots situated along linear transects within each study site. This was estimated visually as the percentage of the area surrounding each point (radius of 100 m) covered by vegetation for four separate layers (the herb layer up to 1 m, shrub layer between 1–3 m, large shrub and small tree layer between 3–5 m, and tree layer above 5 m) similarly as, e.g., in Reif et al. (2006). The relative cover for these four layers was then summed to get an overall relative cover (i.e. it can be higher than 100%; Table 1).

We then placed 100 artificial ground nests along each vegetation plot transect, with one chicken egg put in the middle of an artificially made shallow depression in the ground (about 20 cm in diameter). The artificial nests thus did not simulate complete natural nests of any species. They rather resembled a clutch at the beginning of its formation. Brown chicken eggs are reported to be suitable for ground nest studies because of inconspicuous colouration (Yahner and Mahan 1996) and were used also in other studies on African birds (Carlson and Hartman 2001). However, chicken eggs are larger and more durable than those of small passerines and it can be difficult for some small predators (e.g. mice) to break into them (cf. DeGraaf and Maier 1996). Consequently, the guild of small predators is presumably excluded from our experiment and potential differences in the importance of small predators among study sites may influence our results. Nevertheless, estimates of predation rates on nests of avian species laying larger eggs are not affected. We used artificial ground nests because ground-nesting birds (in contrast to shrub or tree-nesting birds) occur naturally at all study sites and form an important component of local avian communities (Hockey et al. 2005, DS et al. unpublished data). Moreover, ground nests generally experience high nest predation (Ricklefs 1969, Söderström 1999), which allowed us to reveal significant differences between the study sites after a relatively short period of exposure. We placed nests systematically 300 m apart from each other, and determined distances between them using a global positioning system (Garmin GPSMAP 60 CX). All nests were further marked by a small piece of red tape, which we placed on the vegetation about 3 m away from the nest. We avoided placing flags closer to the nests as they might have attracted predators (Green 2004). We controlled for nest visibility and location by consistently placing them in places with no overhead cover (100% visibility from above) and outside the vegetation. We checked all the nests and recorded their fate after 8 d of exposure. We distinguished three categories of nest condition: (1) the egg remained untouched in the nest, (2) egg shell remnants present in the nest, and (3) egg absent. In the course of analyses, nests in the first category were classified as 'unpredated' and nests in the latter two categories as 'predated'. We omitted

Table 1: Basic environmental characteristics of the study sites in South Africa where artificial nest experiments were carried out

Study site name	GPS coordinates	Elevation†	Dates‡	NDVI§	NDVI seasonality††	Habitat‡‡	Cover§§
Pofadder	29°07′40″ S, 19°23′46″ E	988	7–15 Nov	0.1229	0.0024	Kr	21.4
Molopo	25°48′02″ S, 22°53′10″ E	1 000	25 Nov–3 Dec	0.1836	0.0280	Ka	54.3
Kuruman	27°27′42″ S, 23°25′52″ E	1 324	14–22 Nov	0.2176	0.0452	aSW	106.5
Marakele	24°28′45″ S, 27°32′32″ E	1 450	29 Nov–8 Dec	0.3384	0.1436	mSW	150.5
Punda Maria	22°41′29″ S, 31°00′39″ E	482	11–20 Dec	0.3304	0.1183	mSW	151.8

† Approximate elevation above sea level (m)
‡ Dates of artificial nest exposure in 2009
§ Normalised difference vegetation index estimated in January
†† Absolute difference between mean normalised difference vegetation indices estimated in January and July
‡‡ Habitat type: Kr = Karoo, Ka = Kalahari, aSW = arid savanna woodland, mSW = moist savanna woodland
§§ Relative vegetation cover (sum of four vegetation layers in %)

one nest from the analyses (placed in Marakele) because it may have been destroyed by human activity (DH et al. pers. obs.). We compared nest predation estimates among study sites using chi-square statistics.

To investigate spatial variation in avian clutch size across South Africa, we compiled information about all breeding bird species found in 0.25 × 0.25 degree grid cells from Hockey et al. (2005). For each grid cell, we calculated the mean clutch size of birds occurring there. We tested the differences in average clutch sizes among our study sites using mean assemblage clutch size values for 21–25 grid cells (according to the availability of data) surrounding each location. In order to filter out a taxonomic (phylogenetic) effect in geographical distribution of avian clutch sizes we performed ANOVA with a family as an explanatory factor. Then we used residuals from this analysis as well as raw clutch size data for further calculations. As we carried out artificial nest experiments on ground nests, we restricted the data set to bird species classified as ground and near ground nesters (see Appendix 1). Ground nesters have typically a simple nest placed directly on the ground (e.g. francolins, guineafowls, bustards, ostriches or nightjars). Near-ground nesters build more sophisticated structures located up to 30 cm above the ground in a clump of grass or small bushes (e.g. larks, pipits and cisticolas). The differences in clutch size among study sites were tested by analysis of variance (ANOVA) and Tukey's honestly significant difference (HSD) test.

Data processing and the statistical analyses were performed in R 2.12.0 (R Development Core Team 2010), and spatial patterns in clutch size were visualised in SAM software (Rangel et al. 2006). The group data are presented as mean ± SE of mean.

Results

Estimated predation rate differed among study sites being highest in Pofadder (92%), the site with the lowest NDVI. All other study sites showed similar predation rates (Molopo 33%, Kuruman 42%, Marakele 36.4% and Punda Maria 32%). We tested differences in artificial nest predation between pairs of study sites. Our results show that the highest nest predation rate in Pofadder is significantly different from the other sites (all $p < 0.001$; Figure 1a, Table 2). All other comparisons between study sites were insignificant (Table 2) We performed a *post-hoc* analysis and tested the difference between Pofadder and four remaining sites aggregated into one. The analysis revealed again a significant difference ($\chi^2 = 101.22$, df = 1, $p < 0.001$).

In addition, we investigated differences in clutch size among study sites. In the first step, we analysed the clutch size variation for ground and near-ground nesters separately. As the analyses revealed a similar pattern, we pooled both groups into one. We also attempted to control for effect of taxonomy in geographical variation in clutch sizes. The inclusion of such an effect did not influence the results. Still, the analyses presented here are based on clutch size data controlled for taxonomy. We found an increasing trend in average clutch size of avian assemblages from sites of low to high productivity: Pofadder 2.81 ± 0.10 ($n = 21$), Molopo 3.01 ± 0.05 ($n = 25$), Kuruman 3.57 ± 0.10 ($n = 25$), Marakele 3.74 ± 0.03 ($n = 25$), and Punda Maria 3.72 ± 0.04 ($n = 23$). The overall differences were statistically significant (ANOVA: $F_{4,114} = 51.17$, $p < 0.001$; Figure 1b). *Post-hoc* comparisons showed that birds living at the two sites with lowest estimates of NDVI (Pofadder and Molopo) had the lowest mean assemblage clutch size that did not differ from each other (Tukey HSD test: $p = 0.604$). However, both sites differed from the three remaining sites with higher NDVI estimates which had significantly larger clutch sizes (Tukey HSD test: all $p < 0.001$; Figure 1b). The two most productive sites did not differ in clutch size from each other but had significantly higher clutch sizes than the site located near Kuruman, which has an intermediate productivity estimate (both $p < 0.05$; Figure 1b). To illustrate clutch size variation at our study sites in geographical context, we provide Figure 2 that visualise the geographical variation in average clutch size of

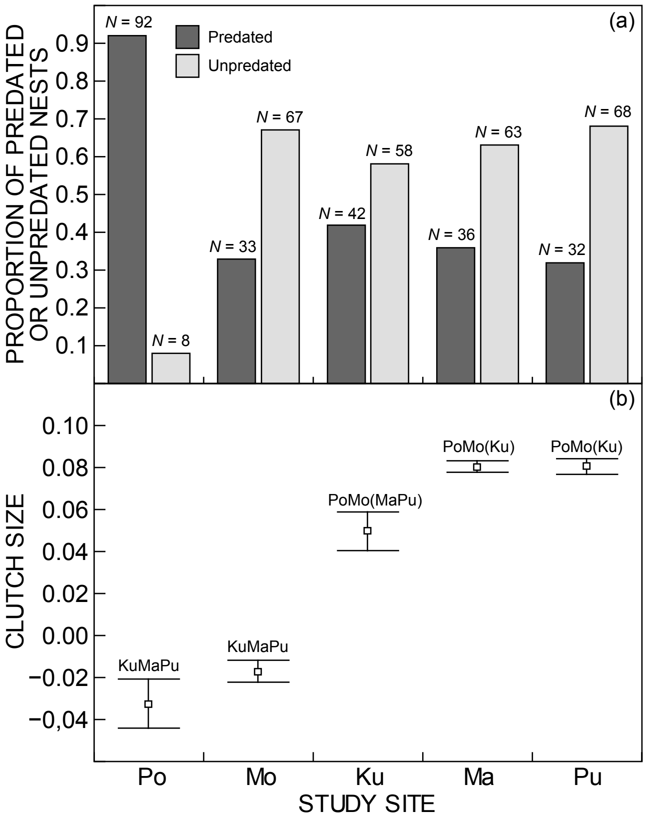


Figure 1: Differences in the proportion of predated (dark bars) and unpredated (pale bars) artificial avian ground nests (a) and in clutch size (b, mean ± SE) of ground and near-ground nesting birds at five study sites located along a gradient of environmental productivity in South Africa: Pofadder (Po), Molopo (Mo), Kuruman (Ku), Marakele (Ma) and Punda Maria (Pu). The overall mean was calculated from average clutch sizes of all members of local avian assemblages within 25 grid cells (or less if the site was located close to the South African border) surrounding each study site. The clutch size data were controlled for taxonomy (see Materials and methods for detail). ANOVA: $F_{4,114} = 51.17$, $p < 0.001$. Significant differences as revealed by Tukey's HSD test are indicated by study sites abbreviations. The demonstrated differences are at the 0.001 and 0.05 (site abbreviations given in parentheses) levels of significance

Table 2: Differences in artificial nest predation rate between pairs of study sites situated along a gradient of environmental productivity in South Africa. χ^2 statistics of 2 × 2 contingency table and statistical significance (in parentheses) are given for each comparison. df = 1 in all cases

	Pofadder	Molopo	Kuruman	Marakele
Pofadder	–			
Molopo	74.26***	–		
Kuruman	56.54***	2.76^{ns}	–	
Marakele	67.10***	0.25^{ns}	0.66^{ns}	–
Punda Maria	76.40***	0.02^{ns}	2.15^{ns}	0.42^{ns}

*** $p < 0.001$, ns = non-significant

ground and near-ground nesters for local bird assemblages across the whole territory of South Africa together with locations of our study sites.

In spite of our sample size limitations, we attempted to relate average clutch size at each study site to its potential determinants (Figure 3). We found that clutch size increased with increasing NDVI ($r^2 = 0.86$, $p = 0.024$) as well as seasonality in NDVI ($r^2 = 0.78$, $p = 0.046$). Nest predation was related to clutch size rather negatively ($r^2 = 0.48$, $p = 0.194$), but the relationship was statistically insignificant and driven by just one point (Pofadder).

Discussion

We aimed to describe relationships among artificial nest predation, environmental productivity, and avian clutch size over a large spatial scale. The highest predation rate took place in the desert site in Pofadder, with almost all nests depredated within 8 d of exposure. Among our study sites, this location had the lowest estimate of environmental productivity and proportion of vegetation cover (both characteristics are highly correlated; Table 1). This suggests a high nest predation rate in sites with low productivity. However, the relationship between estimates of nest predation and estimates of vegetation cover and NDVI is not linear in our study. Instead, some threshold seems to exist in environmental productivity/vegetation cover, above which the nest predation rate is rather similar across different levels of environmental variables. Accordingly, we can divide the sites into two groups: the desert environment in one and several savanna types in the other. Note that such a division is based on differences found at one site and low predation rate in Pofadder, and thus can be a result of site specifics rather than a general property of desert environments.

Similarly high rates of nest predation in arid environments have been reported also in other studies (e.g. Shekedy and Safriel 1992). Higher nest predation rate in arid environments might result from higher predator activity due to (1) higher predator diversity and abundance within a particular environment or (2) greater predator mobility (determined by large home ranges and/or larger areas searched per unit of time) which increases the probability of finding a nest (cf. Schmidt et al. 2006). Also, nest predation rate is influenced by nest concealment, either in terms of microhabitat characteristics surrounding the nest (Martin 1993b) or the overall complexity and heterogeneity of the environment, which may reduce a predator's ability to locate the nest. Indeed, it has been shown that the probability of nest predation is lower in more complex environments with more potential nest sites (Chalfoun and Martin 2009).

Avian nests are predated mostly by mammals, birds and snakes (especially in tropical regions, but also in South Africa; Lloyd 2006). Although we do not have information about the densities of potential nest predators along our gradient, the overall species richness of mammals and birds increases with increasing productivity in South Africa (Bonn et al. 2004, Ceballos and Ehrlich 2006). Higher predator species and functional diversity and abundance may increase the probability of nest predation. This has been one of the basic explanations for the differential predation rate between the tropics and the temperate zone (Skutch 1949; Ricklefs 1969), with potential consequences on the evolution of avian life histories. However, our results do not

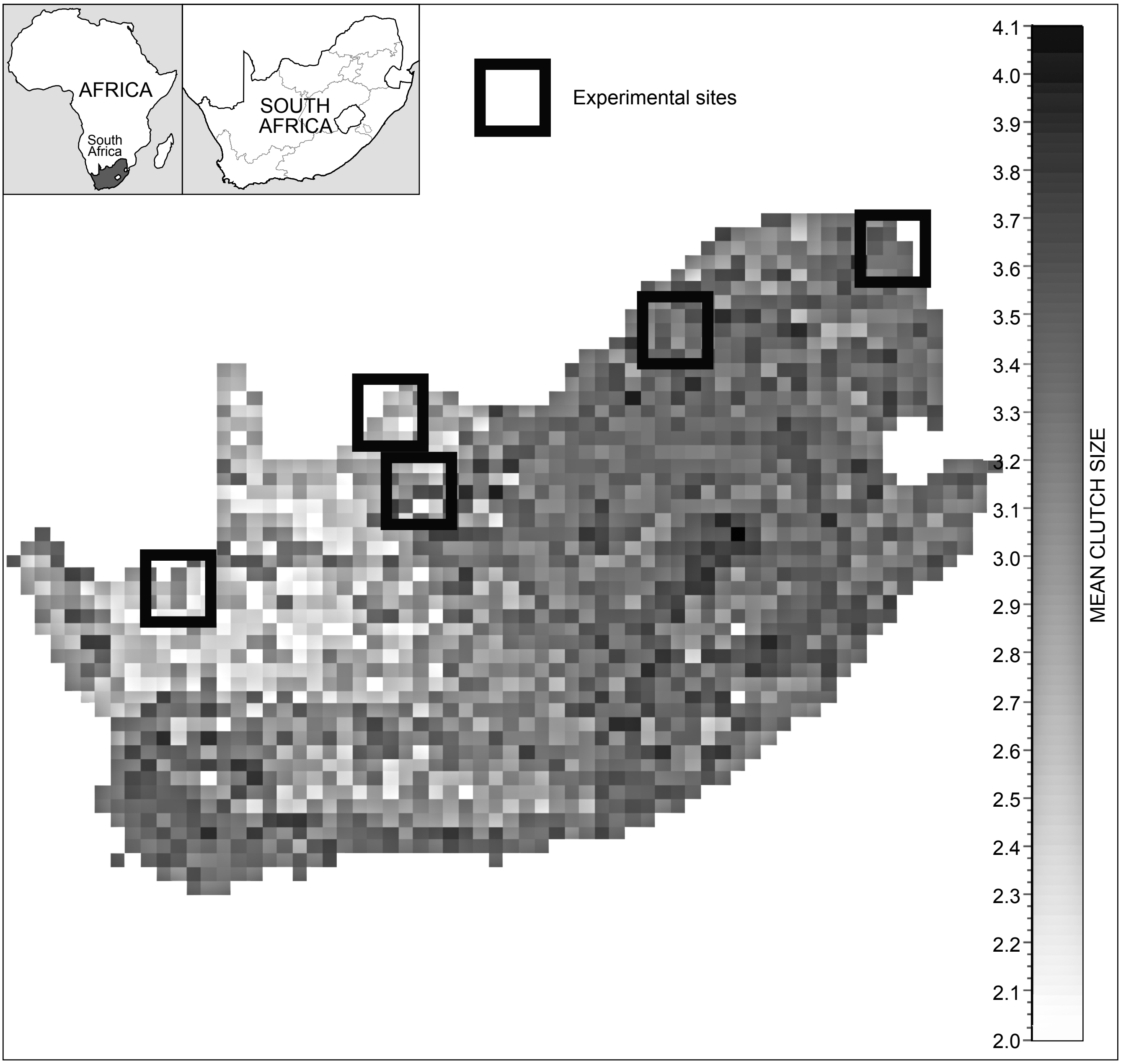


Figure 2: Geographic variation in mean clutch sizes of ground and near-ground nesting representatives of avian assemblages in atlas grid squares in South Africa. Locations of experimental sites are in the centre of black squares

support such an explanation, as the environment that is generally species-poor had the highest predation rate.

Instead, greater predator mobility in arid environments might be responsible for the pattern, as home range size has been reported to decrease with increasing environmental productivity (McLoughlin and Ferguson 2000; Nilsen et al. 2005). Larger home ranges and higher nest visibility in sparsely vegetated arid environments might contribute to a greater probability of predators locating avian nests. Although habitat complexity and heterogeneity was related to environmental productivity, the desert study site near Pofadder was distinctly different from all other sites. There was nearly no vegetation cover at this site (only sparse cover of low bushes and clumps of grass, see Table 1), with consequently more nests being susceptible to predation. Nests were better visible from larger distances and more accessible, and predators thus could scan larger areas than in locations with more vegetation. This could also lie behind the difference in observed nest predation rates between the two least productive sites, Pofadder and Molopo, as the latter one has markedly denser vegetation cover composed of larger bushes. Moreover, arid environments with scarce food resources presumably select for opportunistic feeding strategies (Paltridge 2002), and eggs in avian nests are thus a desirable source of food for a large spectrum of animals.

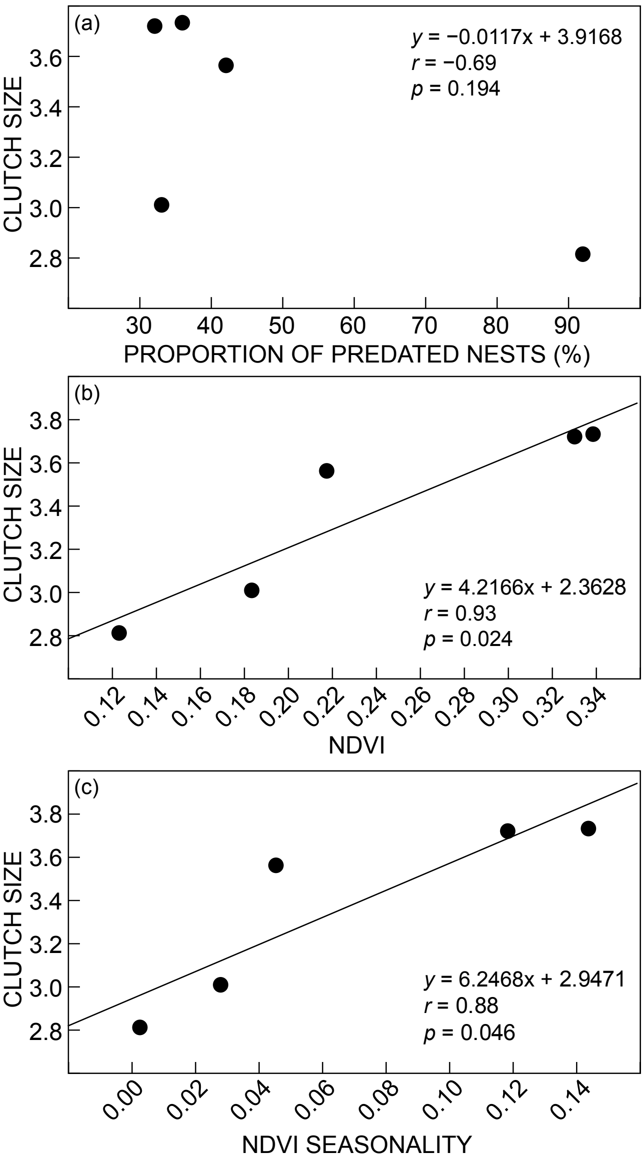


Figure 3: The relationships between mean clutch size of ground and near-ground nesting birds at the five study sites across South Africa and its potential determinants: (a) estimate of nest predation rate; (b) environmental productivity – NDVI estimate in January; and (c) NDVI seasonality – difference between NDVI estimates in January and July

Nest predation is expected to be a strong selective agent in the evolution of avian clutch size (Skutch 1949). In environments with high incidence of nest predation, it is advantageous to limit investment into clutch in order to lower costs of nest failure (Slagsvold 1982) as well as to lower the frequency of nest visits that may attract predators (Skutch 1949). We found that the study site with the highest estimate of nest predation rate (Pofadder) coincided with areas where birds laid the smallest clutches. This suggests a possibility that nest predation is a factor driving evolution of clutch size in South African birds. However, the nest predation rate is not closely related to changes in clutch size across our study sites. Instead, it is constantly low at the majority of them. By contrast, we found rather gradual increase in clutch size from sites with low to high productivity and, moreover, this increase was relatively tightly correlated with both environmental productivity and its seasonality. Similar results have been reported previously by Lepage and Lloyd (2004) on a subset of South African species. These authors attributed the observed geographical variation in clutch size to environmental stochasticity and seasonality in rainfall (rainfall is considered the most important determinant of environmental productivity in South Africa; Zucchini and Adamson 1984). Their explanations are thus based on unpredictability of food availability in arid environments, which forces birds to employ a bet-hedging strategy and lay small clutches. At our study sites, the differences between environmental productivity corresponded to differences in its seasonality. Therefore, we cannot distinguish between the food limitation hypothesis *sensu stricto* (Lack 1947), according to which the total food abundance during breeding season limits clutch size, and 'the seasonality in resources hypothesis' (Ashmole 1963), which states that differences in food availability throughout the year influences clutch sizes of birds via population density effects. Our results suggest that food availability (estimated by NDVI) is most probably responsible for the increase in clutch size of ground-nesting birds along the productivity gradient in South Africa.

We found no statistically significant correlative evidence for the role of nest predation in determining avian clutch size. However, high nest predation rate in a desert location near Pofadder reported by this study may contribute to low clutch sizes of birds observed there. Theoretically, the interaction between low food availability and high nest predation rates may lie behind low clutch sizes of birds in arid environments. Low food availability leading to small clutch size may also enhance nest predation pressure (e.g. by higher frequency of opportunistic feeding strategies of nest predators), which in turn strengthens selection pressure for small clutch size in birds. In such a scenario, one would expect the lowest clutch size in areas with the high nest predation and low food availability. In our study, the two least productive sites (Pofadder and Molopo) differed significantly in predation rate but not in clutch size, although the mean clutch size was slightly lower in Pofadder. This suggests that food availability related to environmental productivity is stronger determinant of clutch size than nest predation at least for our study sites.

Acknowledgements — The study was supported by grants of the Czech Academy of Sciences (project no. IAA601970801), Czech Science Foundation (project no. P505/11/1617) and Ministry of Education, Youth and Sports of the Czech Republic (project nos. LC 06073 and MSM 0021620828). The project was performed with the kind assistance of South African National Parks. We are grateful to local farmers who enabled us to carry out field work within their properties. Anonymous referees greatly improved the manuscript and Andrew McKechnie kindly assisted in editing the text. Irena Šímová helped us with compilation of environmental productivity estimates for South Africa. David Hardekopf improved the English.

References

Albrecht T, Hořák D, Kreisinger J, Weidinger K, Klvaňa P, Michot TC. 2006. Factors determining pochard nest predation along a wetland gradient. *Journal of Wildlife Management* 70: 784–791.

Ashmole, N P. 1963. The regulation of numbers of tropical oceanic birds. *Ibis* 103: 458–473.

Batáry P, Báldi A. 2004. Evidence of an edge effect on avian nest success. *Conservation Biology* 18: 389–400.

Bonn A, Storch D, Gaston KJ. 2004. Structure of the species-energy relationship. *Proceedings of the Royal Society B: Biological Sciences* 271: 1685–1691.

Carlson A, Hartman G. 2001. Tropical forest fragmentation and nest predation – an experimental study in an Eastern Arc montane forest, Tanzania. *Biodiversity and Conservation* 10: 1077–1085.

Ceballos G, Ehrlich PR. 2006. Global mammal distributions, biodiversity hotspots, and conservation. *Proceedings of the National Academy of Sciences of the USA* 103: 19374–19379.

Chalfoun AD, Martin TE. 2009. Habitat structure mediates predation risk for sedentary prey: experimental tests of alternative hypotheses. *Journal of Animal Ecology* 78: 497–503.

Green RE. 2004. Breeding biology. In: Sutherland WJ, Newton I, Green RE (eds), *Bird ecology and conservation: a handbook of techniques*. Oxford: Oxford University Press. pp 57–84.

DeGraaf RM, Maier TJ. 1996. Effect of egg size on predation by white-footed mice. *Wilson Bulletin* 108: 535–539.

Hockey PAR, Dean WRJ, Ryan PG (eds). 2005. *Roberts birds of southern Africa* (7th edn). Cape Town: Trustees of the John Voelcker Bird Book Fund.

Jetz W, Sekercioglu CH, Böhning-Gaese K. 2008. The worldwide variation in avian clutch size across species and space. *PLoS Biology* 6(12), e303. doi:10.1371/journal.pbio.0060303.

Kerley GIH. 1992. Ecological correlates of small mammal community structure in the semiarid Karoo, South Africa. *Journal of Zoology* 227: 17–27.

Kulesza G. 1990. An analysis of clutch-size in New World passerine birds. *Ibis* 132: 407–422.

Lack D. 1947. The significance of clutch-size. *Ibis* 89: 302–352.

Lahti DC. 2001. The “edge effect on nest predation” hypothesis after twenty years. *Biological Conservation* 99: 365–374.

Lepage D, Lloyd P. 2004. Avian clutch size in relation to rainfall seasonality and stochasticity along an aridity gradient across South Africa. *Ostrich* 75: 259–268.

Lloyd P. 2006. Density-dependent nest predation: a field test. *African Journal of Ecology* 44: 293–295.

López-Flores V, MacGregor-Fors I, Schondube JE. 2009. Artificial nest predation along a Neotropical urban gradient. *Landscape and Urban Planning* 92: 90–95.

Martin TE. 1993a. Nest predation among vegetation layers and habitat types: revising the dogmas. *American Naturalist* 141: 897–913.

Martin TE. 1993b. Nest predation and nest sites: new perspectives on old patterns. *BioScience* 43: 523–532.

Martin TE. 1995. Avian life history evolution in relation to nest sites, nest predation, and food. *Ecological Monographs* 65: 101–127.

McKinnon L, Smith PA, Nol E, Martin JL, Doyle FI, Abraham KF, Gilchrist HG, Morrison RIG, Bêty J. 2010. Lower predation risk for migratory birds at high latitudes. *Science* 327: 326–327.

McLoughlin PD, Ferguson SH. 2000. A hierarchical pattern of limiting factors helps explain variation in home range size. *Écoscience* 7: 123–130.

Nilsen EB, Herfindal I, Linnell JDC. 2005. Can intra-specific variation in carnivore home-range size be explained using remote-sensing estimates of environmental productivity? *Écoscience* 12: 68–75.

Paltridge R. 2002. The diets of cats, foxes and dingoes in relation to prey availability in the Tanami Desert, Northern Territory. *Wildlife Research* 29: 389–403.

R Development Core Team 2010. R: a language and environment for statistical computing. Vienna: R Foundation for Statistical Computing.

Rangel TFLVB, Diniz-Filho JAF, Bini LM. 2006. Towards an integrated computational tool for spatial analysis in macroecology and biogeography. *Global Ecology and Biogegraphy* 15: 321–327.

Reif J, Hořák D, Sedláček O, Riegert J, Pešata M, Hrázský Z, Janeček Š, Storch D. 2006. Unusual abundance-range size relationship in an Afromontane bird community: the effect of geographical isolation? *Journal of Biogeography* 33: 1959–1968.

Ricklefs RE. 1969. An analysis of nesting mortality in birds. *Smithsonian Contributions to Zoology* 9: 1–48.

Ricklefs RE. 1980. Geographical variation in clutch size among passerine birds: Ashmole’s hypothesis. *Auk* 97: 38–49.

Schmidt KA, Ostfeld RS, Smyth KN. 2006. Spatial heterogeneity in predator activity, nest survivorship, and nest-site selection in two forest thrushes. *Oecologia* 148: 22–29

Shekedy Y, Safriel UN. 1992. Nest predation and nestling growth rate of two lark species in the Negev Desert, Israel. *Ibis* 134: 268–272.

Sibley CG, Monroe BL. 1990. *Distribution and taxonomy of birds of the world*. New Haven: Yale University Press.

Skutch AF. 1949. Do tropical birds rear as many young as they can nourish? *Ibis* 91: 430–455.

Skutch AF. 1985. Clutch size, nesting success, and predation on nests of tropical birds, reviewed. In: Buckley PA, Foster MS, Morton ES, Ridgely RS, Buckley FG (eds), *Neotropical ornithology*. *Ornithological Monographs* vol. 36. Washington, DC: American Ornithologists Union. pp 575–603.

Slagsvold T. 1982. Clutch size variation in passerine birds: the nest predation hypothesis. *Oecologia* 54: 159-169.

Söderström B. 1999. Artificial nest predation rates in tropical and temperate forests: a review of the effects of edge and nest site. *Ecography* 22: 455–463.

Spanhove T, Lehouck V, Lens L. 2009. Inverse edge effect on nest predation in a Kenyan forest fragment: an experimental case study. *Bird Conservation International* 19: 367–378.

Yahner RH, Mahan CG. 1996. Effects of egg type on depredation of artificial nests. *Wilson Bulletin* 108: 129–136.

Zucchini W, Adamson PT. 1984. *The occurrence and severity of droughts in South Africa*. WRC Report no. 91/1/84. Pretoria: Water Research Commission.

Received March 2011, accepted July 2011
Editor: AE McKechnie

Appendix 1: List of ground and near-ground nesting species included in the clutch size analysis, grouped by study sites and families (following Sibley and Monroe 1990)

Pofadder

Struthionidae: *Struthio camelus*; Phasianidae: *Pternistis capensis, P. afer, Coturnix coturnix;* Numididae: *Numida meleagris;* Anatidae: *Alopochen aegyptiaca, Anas undulata, A. sparsa, A. capensis, A. erythrorhyncha, A. lithii, Netta erythrophthalma, Plectropterus gambensis, Oxyura maccoa;* Strigidae: *Bubo capensis, B. Africanus;* Caprimulgidae: *Caprimulgus rufigena;* Otididae: *Ardeotis kori, Neotis ludwigii, Eupodotis vigorsii, Afrotis afra;* Rallidae: *Rallus caerulescens, Fulica cristata;* Pteroclidae: *Pterocles namaqua, Pterocles bicinctus;* Burhinidae: *Burhinus capensis;* Charadriidae: *Charadrius pallidus, C. pecuarius, C. tricollaris, Vanellus coronatus, V. armatus, Recurvirostra avosetta, Himantopus himantopus;* Glareolidae: *Cursorius rufus, Rhinoptilus africanu;* Accipitridae: *Circus maurus;* Podicipedidae: *Tachybaptus ruficollis;* Ardeidae: *Ardea goliath;* Phoenicopteridae: *Phoenicopterus ruber;* Muscicapidae: *Oenanthe pileata, Cercomela tractrac, C. sinuata, C. schlegelii, Cossypha caffra, Cercotrichas coryphaeus;* Cisticolidae: *Euryptila subcinnamomea, Cisticola juncidis, C. subruficapilla;* Motacilidae: *Motacilla aguimp, M. capensis, Anthus cinnamomeus, A. similis, A. crenatus;* Sylviidae: *Eremomela gregalis;* Alaudidae: *Mirafra apiata, Calendulauda africanoides, C. sabota, C. burra, Certhilauda curvirostris, Chersomanes albofasciata, Calandrella cinerea, Spizocorys conirostris, Spizocorys sclateri, Spizocorys starki, Galerida magnirostris, Eremopterix leucotis, E. verticalis, E. australis;* Passeridae: *Lagonosticta senegala, Estrilda astrild*; Fringillidae: *Emberiza capensis, E. impetuani*

Molopo

Struthionidae: *Struthio camelus*; Phasianidae: *Scleroptila levaillantoides, Pternistis adspersus, Coturnix coturnix, C. delegorguei*; Numididae: *Numida meleagris*; Anatidae: *Alopochen aegyptiaca, A. erythrorhyncha*; Strigidae: *Bubo africanus*; Caprimulgidae: *Caprimulgus rufigena*; Otididae: *Ardeotis kori, Lophotis ruficrista, Afrotis afra*; Rallidae: *Porzana pusilla, Fulica cristata*; Pteroclidae: *Pterocles namaqua, P. burchelli, P. bicinctus*; Burhinidae: *Burhinus capensis*; Charadridae: *Charadrius pecuarius, C. tricollaris, Vanellus coronatus, V. armatus, Himantopus himantopus*, Glareolidae: *Cursorius rufus, C. temminckii*, *Rhinoptilus africanus*, Accipitridae: *Circus maurus*; Podicipedidae: *Tachybaptus ruficollis*; Muscicapidae: *Oenanthe pileata, Saxicola torquatus, Cercotrichas paena*; Cisticolidae: *Cisticola aridulus, C. rufilatus*; Alaudidae: *Mirafra passerina, M. africana, M. apiata, Calendulauda africanoides, C. sabota, Chersomanes albofasciata, Calandrella cinerea, Spizocorys conirostris, Eremopterix leucotis, E. verticalis*; Passeridae: *Motacilla capensis*, *Anthus cinnamomeus, A. vaalensis, Lagonosticta senegala, Estrilda astrild;* Fringillidae: *Emberiza tahapisi, E. impetuani*

Kuruman

Struthionidae: *Struthio camelus*; Phasianidae: *Scleroptila levaillantoides, Pternistis adspersus, P. swainsonii, Coturnix coturnix*; Numididae: *Numida meleagris*; Dendrocygnidae: *Dendrocygna viduata, D. bicolor*; Anatidae: *Thalassornis leuconotus, Alopochen aegyptiaca, A. undulata, A. sparsa, A. capensis, A. hottentota, A. erythrorhyncha, A. smithii, Netta erythrophthalma, Plectropterus gambensis, Oxyura maccoa*; Turnicidae: *Turnix sylvaticus*; Caprimulgidae: *Caprimulgus rufigena*; Otididae: *Ardeotis kori, Neotis ludwigii, Lophotis ruficrista, Afrotis afra*; Gruidae: *Anthropoides paradiseus*; Rallidae: *Rallus caerulescens, Amaurornis flavirostris, Porphyrio madagascariensis, Gallinula chloropus, Fulica cristata*; Pteroclidae: *Pterocles namaqua, P. burchelli, P. bicinctus*; Strigidae: *Bubo africanus*; Scolopacidae: *Gallinago nigripennis*; Burhinidae: *Burhinus capensis*; Charadriidae: *Charadrius pecuarius, C. tricollaris, Vanellus coronatus, V. armatus, Recurvirostra avosetta, Himantopus himantopus*; Glareolidae: *Cursorius rufus, C. temminckii, Rhinoptilus africanus, R. chalcopterus*; Laridae: *Larus cirrocephalus*; Accipitridae: *Circus maurus, C. ranivorus*; Podicipedidae: *Podiceps cristatus, Tachybaptus ruficollis*; Phoenicopteridae: *Phoenicopterus ruber, P.minor*; Threskiornithidae: *Plegadis falcinellus*; Muscicapidae: *Oenanthe pileata, Saxicola torquatus, Cossypha caffra, Cercotrichas coryphaeus, C. paena*; Cisticolidae: *Cisticola juncidis, C. aridulus, C. rufilatus, C. chiniana, C. tinniens, C. fluvicapilla*; Alaudidae: *Mirafra passerina, M. africana, M. apiata, Calendulauda africanoides, C. sabota, Chersomanes albofasciata, Calandrella cinerea, Spizocorys conirostris, Eremopterix verticalis*; Passeridae: *Motacilla aguimp, M. capensis, Anthus cinnamomeus, A. similis, A. vaalensis, Macronyx capensis*, *Lagonosticta senegala, Estrilda astrild, Ortygospiza atricollis, Euplectes afer, E. progne*; Fringilidae: *Emberiza capensis, E. tahapisi, E. impetuani*

Marakele

Struthionidae: *Struthio camelus*; Phasianidae: *Peliperdix coqui, Dendroperdix sephaena, Scleroptila shelleyi, Pternistis natalensis, Pternistis swainsonii,Coturnix coturnix, C. Delegorguei*; Numididae: *Numida meleagris*; Dendrocygnidae: *Dendrocygna viduata;* Anatidae: *Thalassornis leuconotus, Alopochen aegyptiaca, A. undulata, A. sparsa, A. hottentota, A. erythrorhyncha, A. smithii, Netta erythrophthalma, Plectropterus gambensis, Oxyura maccoa*; Turnicidae: *Turnix sylvaticus*; Strigidae: *Asio capensis, Bubo africanus*; Caprimulgidae: *Caprimulgus pectoralis, C. rufigena*; Otididae: *Ardeotis kori, Neotis denhami, Eupodotis senegalensis, Lophotis ruficrista, Afrotis afra*; Gruidae: *Anthropoides paradiseus*; Heliornithidae: *Podica senegalensis*; Rallidae: *Rallus caerulescens, Crecopsis egregia, Amaurornis flavirostris, Sarothrura rufa, Porphyrio madagascariensis, Gallinula chloropus, Fulica cristata*; Pteroclidae: *Pterocles burchelli, P. gutturalis, P. bicinctus*; Scolopacidae: *Gallinago nigripennis*; Rostratulidae: *Rostratula benghalensis*; Jacanidae: *Actophilornis africanus*; Burhinidae: *Burhinus capensis, B. vermiculatus*; Glareolidae: *Cursorius temminckii, Rhinoptilus chalcopterus*; Charadriidae*: Charadrius marginatus, C. pecuarius, C. tricollaris*, *Vanellus coronatus, V. armatus, V. senegallus, Recurvirostra avosetta, Himantopus himantopus*; Laridae: *Larus cirrocephalus, Chlidonias hybrida*; Accipitridae: *Circus ranivorus*; Podicipedidae: *Podiceps cristatus, Tachybaptus ruficollis*; Ardeidae: *Ardea goliath,* Phoenicopteridae: *Phoenicopterus ruber, P. minor*; Threskiornithidae: *Plegadis falcinellus*; Muscicapidae: *Oenanthe pileata, O.bifasciata, Saxicola torquatus, Cossypha caffra, C. humeralis, Cercotrichas leucophrys, C. paena*; Cisticolidae: *Cisticola juncidis, C. aridulus, C. textrix, C. ayresii, C. rufilatus, C. chiniana, C. tinniens, C. aberrans, C. fulvicapilla*; Sylviidae: *Camaroptera brachyura, Sphenoeacus afer, Bradypterus baboecala*; Alaudidae: *Mirafra passerina, M. africana, M. rufocinnamomea, Calendulauda africanoides, C. sabota, Certhilauda chuana, Calandrella cinerea, Spizocorys conirostris, Eremopterix leucotis, E. verticalis*; Passeridae: *Motacilla aguimp, M. capensis, Anthus cinnamomeus, A. similis, A. leucophrys, A. vaalensis, A. lineiventris, A.caffer, Macronyx capensis, Euplectes afer, E. albonotatus, E. progne, Lagonosticta rhodopareia, L. senegala, Estrilda astrild, Ortygospiza atricollis, Sporaeginthus subflavus*; Fringillidae: *Emberiza capensis, E. tahapisi, E. impetuani*

Punda Maria

Struthionidae: *Struthio camelus*; Phasianidae: *Peliperdix coqui, Dendroperdix sephaena, Scleroptila shelleyi, Pternistis natalensis, P. swainsonii, Coturnix coturnix, C. delegorguei*; Numididae: *Numida meleagris, Guttera edouardi*; Turnicidae: *Turnix sylvaticus*; Dendrocygnidae: *Dendrocygna viduata, D. bicolor;* Anatidae: *Thalassornis leuconotus, Alopochen aegyptiaca, A. undulata, A. sparsa, A. hottentota, A. erythrorhyncha, Netta erythrophthalma, Plectropterus gambensis*; Centropidae: *Centropus grillii*; Strigidae: *Asio capensis, Bubo africanus*; Caprimulgidae: *Caprimulgus pectoralis, C. rufigena, C. fossii, Macrodipteryx* vexillarius; Otididae: *Ardeotis kori, Lophotis ruficrista, Lissotis melanogaster*; Heliornithidae: *Podica senegalensis*; Rallidae: *Crecopsis egregia, Amaurornis flavirostris, Porzana pusilla, Sarothrura elegans, Porphyrio madagascariensis, P. alleni, Gallinula chloropus, G. angulata,Fulica cristata*; Pteroclidae: *Pterocles bicinctus*; Scolopacidae: *Gallinago nigripennis*; Rostratulidae: *Rostratula benghalensis*; Jacanidae: *Actophilornis africanus*, *Microparra capensis*; Burhinidae: *Burhinus capensis, B. vermiculatus*; Charadriidae: *Charadrius marginatus, C. pallidus, C. pecuarius, C. tricollaris, Vanellus coronatus, V. lugubris, V. armatus, V. albiceps, V. senegallus, Recurvirostra avosetta, Himantopus himantopus*; Glareolidae: *Cursorius temminckii, Rhinoptilus chalcopterus, Glareola pratincola*; Laridae: *Larus cirrocephalus*, *Sterna caspia, Chlidonias hybrida*; Accipitridae: *Circus ranivorus*; Podicipedidae: *Podiceps nigricollis, Tachybaptus ruficollis*; Ardeidae: *Ardea goliath*; Phoenicopteridae: *Phoenicopterus ruber*; Threskiornithidae: *Plegadis falcinellus*; Pelecanidae: *Pelecanus onocrotalus*; Muscicapidae: *Oenanthe pileata, Saxicola torquatus, Cossypha caffra, C. humeralis*; *Pogonocichla stellata, Cercotrichas leucophrys, C. paena*; Megaluridae: *Bradypterus baboecala*; Cisticolidae: *Cisticola juncidis, C. aridulus, C. ayresii, C. lais, C. chiniana, C. erythrops, C. galactotes, C. tinniens, C. natalensis, C. aberrans, C. fulvicapilla*; Sylviidae: *Phylloscopus ruficapilla, Camaroptera brachyura, Sphenoeacus afer*; Alaudidae: *Mirafra passerina, M. africana, M. rufocinnamomea, Calendulauda africanoides, C. sabota, C. cinerea, Eremopterix leucotis*; Passeridae: *Motacilla aguimp, M. capensis, Anthus cinnamomeus, A. similis, A. leucophrys, A. vaalensis, A. lineiventris, A. caffer, Macronyx croceus, Euplectes afer, E. capensis, E. albonotatus, Hypargos margaritatus, Lagonosticta rhodopareia, L. senegala, Estrilda astrild, Ortygospiza atricollis, Sporaeginthus subflavus*; Fringillidae: *Emberiza tahapisi, E. impetuani*

Chapter 2

Global Ecology and Biogeography, (Global Ecol. Biogeogr.) (2015) **24**, 437–447

Global Ecology and Biogeography A Journal of Macroecology

RESEARCH PAPER

Relative food limitation drives geographical clutch size variation in South African passerines: a large-scale test of Ashmole's seasonality hypothesis

David Hořák[1,*], Anna Tószögyová[1,2] and David Storch[1,2]

[1]*Department of Ecology, Faculty of Science, Charles University in Prague, Viničná 7, CZ-128 44 Praha 2, Czech Republic,* [2]*Center for Theoretical Study, Charles University and the Academy of Sciences of the Czech Republic, Jilská 1, CZ-110 00 Praha 1, Czech Republic*

ABSTRACT

Aim To separate the effect of overall resource level from the effect of seasonality on avian clutch size to test Ashmole's hypothesis that birds have larger clutch sizes in seasonal environments due to high per capita food availability during the breeding season.

Location South Africa and Lesotho.

Methods We used a large-scale environmental gradient to test the effects of maximum resource availability and resource seasonality (estimated by the normalized difference vegetation index) on clutch size variation among local passerine assemblages (25 km × 25 km grid cells). The importance of maximum resource availability was distinguished from the importance of resource seasonality by using multivariate general additive models and by subsetting the data so that variation in one of these parameters was minimized. Spatial autocorrelation was controlled for by using spatial generalized least squares.

Results Assemblage mean clutch size showed a hump-shaped relationship with maximum resource availability but an increase with resource seasonality. When the variation in maximum resource availability was fixed, clutch size increased with increasing seasonality, but it decreased with increasing maximum resource availability when we fixed the variation in seasonality. These results hold for all feeding guilds except granivores, for which we found opposite patterns. The patterns were much less pronounced when family membership was controlled for, indicating that the overall trends are mostly driven by variation between families.

Main conclusions Although clutch size can be affected by many factors related to environmental productivity and its variation, Ashmole's hypothesis provides the most parsimonious explanation of the observed patterns: geographical patterns in mean clutch size across bird assemblages seem to be driven by variation of per capita food availability determined by seasonal variation of population density.

Keywords

Avian assemblages, David Lack, macroecological approach, normalized difference vegetation index, number of eggs, Philip Nelson Ashmole.

*Correspondence: David Hořák, Department of Ecology, Faculty of Science, Charles University in Prague, Viničná 7, CZ-128 44 Praha 2, Czech Republic.
E-mail: david.horak@natur.cuni.cz

INTRODUCTION

Clutch size is a key demographic trait in avian biology. Its variation has attracted much scientific attention since the work of David Lack, who established an evolutionary perspective in ecology in the middle of the last century (Lack, 1947, 1948). The most striking geographical pattern in clutch size is observed along latitude: tropical birds tend to produce smaller clutches than their temperate zone counterparts (Moreau, 1944; Jetz *et al*., 2008). Many hypotheses have been proposed to explain this observation. Smaller clutches in the tropics are frequently attributed to higher rates of nest predation (Skutch, 1949), lower

DOI: 10.1111/geb.12261

food availability during breeding (Slagsvold, 1975), an adjustment of reproductive effort to the probability of future reproduction (Moreau, 1944; Williams, 1966; Martin, 2002) or even a lower availability of calcium necessary for the production of eggshells (Patten, 2007). The effect of resource availability on clutch size has been tested most often (e.g. Ricklefs, 1980; Koenig, 1984; Jetz *et al.*, 2008; Hořák *et al.*, 2011), and it has already been validated at a global scale (Jetz *et al.*, 2008). The popularity of the 'food limitation hypothesis' is not surprising, as it was first formulated by Lack (1947) himself who believed that the number of eggs within a clutch corresponds to the number of young that the parents can nourish, determined by the amount of food available. The hypothesis thus seems to imply that larger clutches are to be expected in food-rich environments. However, the situation is more complicated. Ashmole (1963) suggested that it is not the total amount of food available, but the amount relative to population density that affects clutch size. He proposed that population densities are determined during periods when food is scarce (i.e. during winter time in the temperate zone), while clutch size is determined by per capita food availability during the breeding season (i.e. spring time in the temperate zone). Clutch size is thus expected to be higher in places where food is scarce during the harsh period of the year (when population numbers decline) and abundant during the breeding season (low population densities lead to high food resources available per capita). Consequently, the larger the difference between maximum and minimum resource availability in the course of the year – a seasonality *sensu* Ashmole (1963) (see Fig. 1) – the larger clutches should be.

Although the seasonality of food availability has been linked to clutch size in a number of studies (Lack & Moreau, 1965; Ricklefs, 1980; Lepage & Lloyd, 2004; Jetz *et al.*, 2008; Hořák *et al.*, 2011), its effect is often interwoven with overall food levels (but see Ricklefs, 1980). This is mostly because the maximum amount of food resources and the seasonality of food availability are highly correlated in natural environments (see, e.g., the supplementary material in Jetz *et al.*, 2008), which hampers the attribution of clutch size variation to one of these factors. More importantly, the effect of the absolute difference between minimum and maximum food levels on clutch size should be considered in relation to overall levels of food abundance. This leads to an additional prediction that, besides increasing clutch size with seasonality, clutch size should decrease with increasing maximum amount of resources under constant seasonality (measured as absolute differences between resource levels in winter versus breeding season). A more food-rich environment should host more abundant populations at the same level of seasonality, which in turn lowers per capita food income during breeding, because the *relative* difference between resource levels in breeding and non-breeding seasons is lower in such a situation (Fig. 1). The effect of relative difference in resource availability could be potentially investigated by testing the effects of the minimum/maximum productivity ratio (cf. Ricklefs, 1980), but since it is not clear whether food availability relates linearly to productivity, the phenomenon is better investigated under fixed levels of environmental variables. This is the approach we take here.

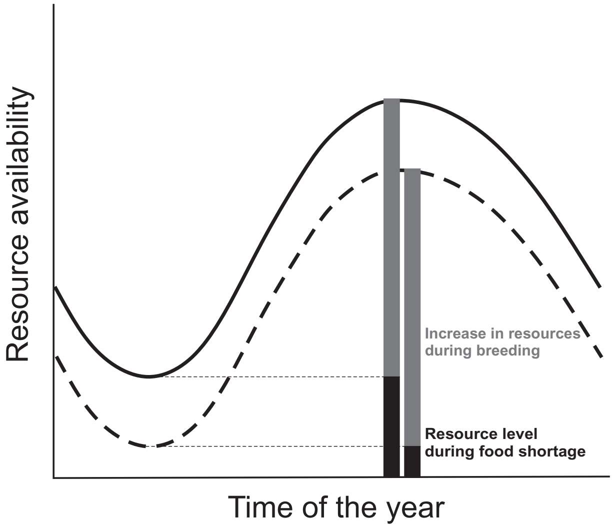


Figure 1 A graphical model of the variation in resource availability during the seasonal cycle between two imaginary locations (solid and dashed curves) that differ in maximum resource level but not in seasonality – an absolute increase in resources between periods of minimum and maximum resource availability (adjusted according to Ricklefs, 1980). Ashmole's hypothesis is based on the assumption that the adult population level is limited by resource availability during the stage of the seasonal cycle when resources are at their minimum. Therefore, per capita energy availability during breeding (resource maximum during the seasonal cycle) depends on its relative increase during the seasonal cycle. Ashmole's hypothesis thus suggests larger clutches at locations indicated by the dashed curve, as relative increment during the breeding season is higher there. Consequently, at fixed levels of seasonality, clutch size should decrease with increasing overall resource levels.

In this study, we focus on birds breeding in South Africa. We restricted the analyses to passerines, as they represent a phylogenetically homogeneous set of species with relatively similar life histories including the mode of energy allocation into reproduction. We used a large-scale gradient of environmental productivity in South Africa, which is convenient for the purpose of our study for two reasons: (1) both productivity and seasonality vary considerably in space, and (2) environmental variation is relatively gradual and situated mostly longitudinally, allowing the implicit filtering out of some biogeographical effects that may affect global-scale variation in avian clutch size.

The aim of this study is to describe geographical patterns in mean clutch size of species assemblages and relate them to variation in the surrogates of resource availability and seasonality. We make the following predictions. If Ashmole's density hypothesis holds, assemblage mean clutch size should (1) increase with seasonality when controlled for overall resource levels, and (2) decrease with maximum resource level during the breeding season when controlled for seasonality (see above; Fig. 1). Additionally, (3) these effects should be more prominent in birds that are dependent on seasonal food resources. In order to separate the effects of environmental variables we:

(1) investigated how residual variation of the maximum productivity–seasonality relationship affects assemblage mean clutch size, and (2) looked separately at selected parts of the productivity gradient within which the variation in one of the focal environmental variables was limited.

METHODS

Species distribution data

Data on the geographical distribution of birds were taken from information collected between 1987 and 1992 as part of the Southern African Bird Atlas Project (Harrison *et al.*, 1997) at 0.25° spatial resolution. All passerine species recorded within each grid cell (*c.* 25 km × 25 km) were considered a local assemblage. The whole territory of South Africa and Lesotho was covered by 1858 grid cells/assemblages.

Clutch size information

From Hockey *et al.* (2005) we collected information about mean clutch sizes for 277 passerine species which breed in South Africa and Lesotho, and for which we had information about their geographical distribution. For each local assemblage, we calculated mean clutch size. We excluded brood parasites, as their clutch sizes are difficult to define, and rarely occurring vagrants, marginal species (occurring in fewer than six grid cells) and species escaped from captivity. The situation might be further complicated by intra-African migrants and vagrants which could avoid seasonal food shortages by moving elsewhere. However, omitting intra-African migrants had no effect on mean assemblage clutch sizes (see Appendix S6 in Supporting Information), so we decided to keep them in the data set. To reveal whether the clutch size patterns were determined by different geographical distributions of the members of passerine families with conservative clutch sizes or by environmentally induced variation of clutch size within families, we tested for the effect of the taxonomic family membership of species as a part of the analyses. We performed ANOVA with family as an explanatory factor. Then we used residuals from this analysis as well as raw clutch size data for further calculations.

Different feeding guilds might utilize different food resources. Therefore, we also performed the analyses separately for three groups of passerines: (1) insectivorous species ($n = 140$), (2) species eating fruits and a combination of fruits and insects ($n = 37$), and (3) species eating grains and a combination of grains and insects ($n = 76$). We omitted nectarivorous ($n = 15$) and omnivorous birds ($n = 9$) from these analyses due to the small number of species within these groups. The information about dietary composition was compiled from Hockey *et al.* (2005).

Environmental productivity information

For each grid cell, we obtained the normalized difference vegetation index (hereafter NDVI), an estimate of the environmental productivity based on the spectral properties of vegetation. Average monthly maxima from the period 1982–2004 were obtained from the 'Africa Data Dissemination Service' data set provided by the United States Geological Survey (http://iridl.ldeo.columbia.edu/SOURCES/.USGS/.ADDS). For each grid cell, the month showing the highest NDVI value was used as an estimate of the maximum environmental productivity (hereafter $\mathrm{NDVI}_{\mathrm{maximum}}$). To estimate environmental seasonality we used the difference between the maximum and minimum NDVI values for each grid cell (hereafter $\mathrm{NDVI}_{\mathrm{seasonality}}$). As NDVI describes the 'greenness' of vegetation and has been shown to be closely correlated with rainfall, total green biomass and net primary productivity (Goward & Dye, 1987; Chong *et al.*, 1993; Paruelo *et al.*, 1997; Schmidt & Karnieli, 2002), we believe that its variation reflects the differences in the amount of food available to birds over large spatial scales. This assumes that the amount of food for breeding, such as arthropod abundance, correlates with overall plant productivity and biomass, as has been suggested, e.g. by Gordo (2007). A positive relationship between arthropod abundance and NDVI has been shown by Lassau & Hochuli (2008) and Lafage *et al.* (2014).

Data analyses

During exploratory analyses we found that $\mathrm{NDVI}_{\mathrm{maximum}}$ and $\mathrm{NDVI}_{\mathrm{seasonality}}$ were strongly related across grid cells in South Africa (Fig. 2). Their mutual relationship was positive and

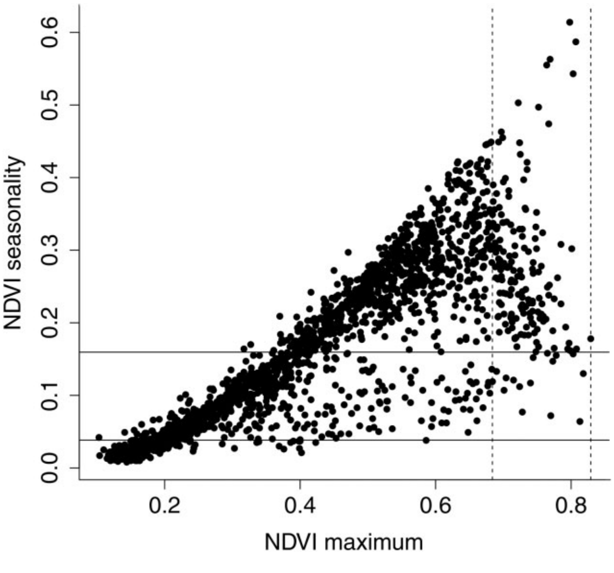


Figure 2 The relationship between maximum normalized difference vegetation index (NDVI) and seasonality in NDVI (the difference between minimum and maximum NDVI) in South Africa. To disentangle the effects of NDVI maximum and NDVI seasonality on avian clutch size, we selected blocks of data in which the variation in one of the environmental variables was limited while the second one varied normally. The blocks of data with limited variation in NDVI seasonality (solid line) and NDVI maximum (dashed line) are depicted.

highly significant ($r = 0.83$, $P < 0.001$). Given such collinearity between explanatory variables, it is difficult to distinguish between the effects of $\text{NDVI}_{\text{maximum}}$ and $\text{NDVI}_{\text{seasonality}}$ (Dormann *et al.*, 2013). We decided to cope with this difficulty using two approaches that at the same time test for the importance of relative values of $\text{NDVI}_{\text{maximum}}$ and $\text{NDVI}_{\text{seasonality}}$.

First, we investigated the effect of the residual variation of the relationship between $\text{NDVI}_{\text{maximum}}$ and $\text{NDVI}_{\text{seasonality}}$ on the variation in assemblage mean clutch size. In order to do this, we took residuals from a linear model [ordinary least squares (OLS) regression] where $\text{NDVI}_{\text{maximum}}$ figured as the response and $\text{NDVI}_{\text{seasonality}}$ as the explanatory variable (hereafter RES1). RES1 residuals highlight places where $\text{NDVI}_{\text{maximum}}$ is higher (positive residuals) or lower (negative residuals) than predicted by $\text{NDVI}_{\text{seasonality}}$. Then, we took residuals from the linear relationship where the environmental variables were reversed in comparison with the previous model, i.e. $\text{NDVI}_{\text{maximum}}$ was the explanatory variable and $\text{NDVI}_{\text{seasonality}}$ was the response variable (hereafter RES2). Thus, RES2 residuals highlight places where $\text{NDVI}_{\text{seasonality}}$ is higher or lower than predicted by $\text{NDVI}_{\text{maximum}}$.

Second, we created two subsets of data containing only ad hoc selected grid cells. In the first subset, we restricted the variation in $\text{NDVI}_{\text{maximum}}$ as much as possible (so that we still had a reasonable sample size) and kept the whole variation in $\text{NDVI}_{\text{seasonality}}$. For this purpose we selected only grid cells for which the $\text{NDVI}_{\text{maximum}}$ values were within the upper 20% of the range (i.e. between 0.6838 and 0.829, delimited by dashed lines in Fig. 2). This subset of data contained 182 grid cells and allowed us to test the effect of $\text{NDVI}_{\text{seasonality}}$ on clutch size at restricted and high levels of $\text{NDVI}_{\text{maximum}}$. In the second subset, we did the opposite and restricted the variation in $\text{NDVI}_{\text{seasonality}}$ in a similar way. However, the lowest values of $\text{NDVI}_{\text{seasonality}}$ are found only in grid cells with the lowest values of $\text{NDVI}_{\text{maximum}}$, which hampers the intention of our analysis. Therefore, to include the whole range of $\text{NDVI}_{\text{maximum}}$ values, we shifted the range of selected grid cells slightly (5%) towards the higher values of $\text{NDVI}_{\text{seasonality}}$ (delimited by solid lines in Fig. 2). As a result, the second subset of data contained grid cells having $\text{NDVI}_{\text{seasonality}}$ values between the lower 5% and 25% of the range (i.e. between 0.0383 and 0.1595). The second subset of data contained 718 grid cells and allowed us to test the effect of $\text{NDVI}_{\text{maximum}}$ on clutch size at restricted and low levels of $\text{NDVI}_{\text{seasonality}}$.

To investigate general patterns in the data we first decided to employ simple linear models. However, exploratory graphical analyses suggested that nonlinear patterns might be hidden within the huge number of data points. For that reason, we repeated the analyses using generalized additive models (hereafter GAM), a useful tool for this purpose as they allow the shape of a relationship to be captured without pre-judging the issue by choosing a particular parametric form (Crawley, 2007).

As our data have spatial structure, we run spatial generalized least squares (GLS) models as an alternative to OLS regression. However, apart from more similar species compositions (and therefore clutch sizes) between nearby grid cells, a strong spatial autocorrelation can be observed in environmental variables along our gradient. Consequently, it is difficult to distinguish between a proximity effect per se and similarities caused by environmental conditions. Thus, we decided to present the results of both non-spatial and spatial models.

Data processing and the statistical analyses were performed in R 3.0.2 (R Development Core Team, 2013) and the GAMs were done using the 'mgcv' R library. Spatial patterns in assemblage mean clutch size were visualized in SAM software (Rangel *et al.*, 2010).

RESULTS

Geographical patterns

Smaller clutches on average were found in arid areas of the transition zone between the arid savanna and Karoo, but also in productive places along the shore of the Indian Ocean and in tropical parts in the eastern part of the country (e.g. Kruger National Park). In contrast, larger clutches characterize central eastern parts of South Africa in the grassland region (see Fig. 3a).

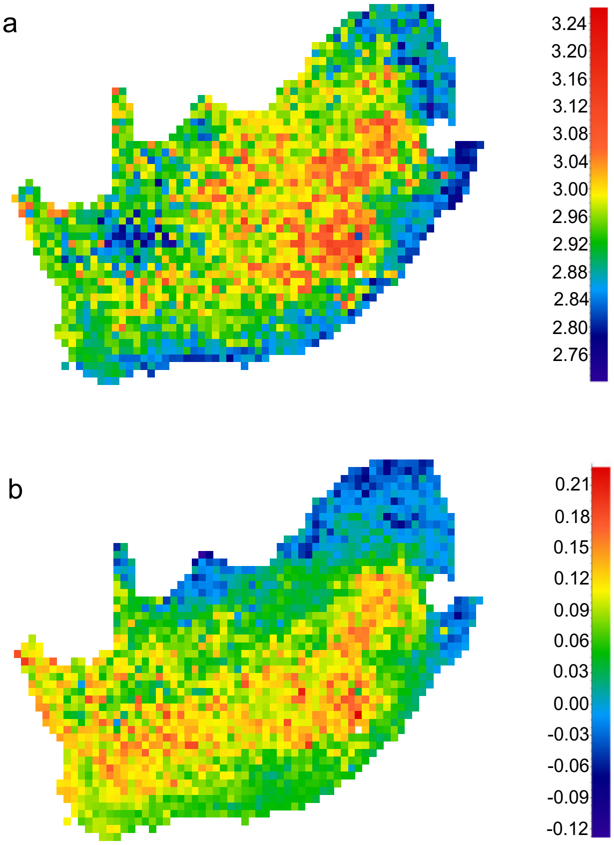


Figure 3 Geographical patterns of assemblage mean clutch size in South African passerines. Geographical variation in raw local assemblage (0.25° × 0.25° grid cell) means (a) and the values obtained after controlling for taxonomy, i.e. membership in passerine families (b).

Linear models

We performed linear models evaluating the effect of $\mathrm{NDVI}_{\mathrm{maximum}}$ and $\mathrm{NDVI}_{\mathrm{seasonality}}$ on assemblage mean clutch size. First, we built a multivariate model of both NDVI variables and their interaction, and subsequently univariate models for each variable separately. Then, we explained the variation in clutch size by RES1 and RES2, respectively. Finally, we tested the relationships using subsetted data. In all tests, we found a significant and negative effect of $\mathrm{NDVI}_{\mathrm{maximum}}$ and a significant and positive effect of $\mathrm{NDVI}_{\mathrm{seasonality}}$ on clutch size. The results were different after controlling for taxonomy. For detailed information see Appendix S1.

Spatial GLS models

The model that included the effects of $\mathrm{NDVI}_{\mathrm{maximum}}$, $\mathrm{NDVI}_{\mathrm{seasonality}}$ and their interaction on clutch size variation explained 18.4% of the total variance (predictors and space together explained 57.2%), and suggested a significant and negative effect of $\mathrm{NDVI}_{\mathrm{maximum}}$ (Std Coeff = –0.278, $t = -3.876$, $P < 0.001$) and a significant but positive effect of $\mathrm{NDVI}_{\mathrm{seasonality}}$ (Std Coeff = 0.675, $t = 4.601$, $P < 0.001$). However, the interaction term of the model was also significant and negative (Std Coeff = –0.444, $t = -2.953$, $P = 0.003$). Further, we ran the same model but with clutch size controlled for taxonomy. It explained 5.2% of the total variance (predictors and space together explained 84%) and revealed a significant and negative effect of $\mathrm{NDVI}_{\mathrm{maximum}}$ (Std Coeff = –0.154, $t = -2.361$, $P = 0.018$). However, neither $\mathrm{NDVI}_{\mathrm{seasonality}}$ (Std Coeff = –0.019, $t = -0.149$, $P = 0.881$) nor the interaction term (Std Coeff = 0.107, $t = 0.799$, $P = 0.424$) were statistically significant in this case.

Univariate analyses

Clutch size was significantly and negatively related to $\mathrm{NDVI}_{\mathrm{maximum}}$, RES1, as well as to $\mathrm{NDVI}_{\mathrm{maximum}}$ within the subset of grid cells with a fixed level of seasonality. However, it was significantly and positively related to $\mathrm{NDVI}_{\mathrm{seasonality}}$ and RES2. We found no significant relationship between clutch size and $\mathrm{NDVI}_{\mathrm{seasonality}}$ within the subset of grid cells with a fixed level of maximum productivity. All the spatial analyses became weaker or non-significant after controlling for taxonomy, which suggests that the majority of clutch size variation is among families (as in the OLS models above). Detailed results for the GLS models are provided in Appendix S2.

Generalized additive models (GAMs)

A model investigating the effect of $\mathrm{NDVI}_{\mathrm{maximum}}$, $\mathrm{NDVI}_{\mathrm{seasonality}}$ and their interaction on clutch size variation explained 36.7% of the variance (generalized cross-validation score = 0.0033). It suggested no significant effect of $\mathrm{NDVI}_{\mathrm{maximum}}$ ($F = 0.421$, $P = 0.765$, estimated d.f. = 3.1) but a significant effect of $\mathrm{NDVI}_{\mathrm{seasonality}}$ ($F = 9.18$, $P = 0.002$, estimated d.f. = 1). However, the interaction term was significant ($F = 5.28$, $P < 0.001$, estimated d.f. = 21.4). The same model with clutch size controlled for taxonomy explained a lower proportion of the total variance (21%, generalized cross-validation score = 0.0024) and none of the terms was statistically significant (all $P > 0.154$).

Univariate analyses

We fitted GAMs evaluating the effects of environmental variables on clutch size separately (Table 1). We found a significant effect of $\mathrm{NDVI}_{\mathrm{maximum}}$ on clutch size ($F = 58.54$, $P < 0.001$, estimated d.f. = 5.71, 18.1% deviance explained). Setting upper limit for d.f.s associated with the smoothing to three caused no significant change in the model deviance ($F = 1.98$, $P = 0.10$). This simplified model explained 17.7% of the deviance ($F = 199.8$, $P < 0.001$, estimated d.f. = 2) and revealed a hump-shaped relationship between clutch size and $\mathrm{NDVI}_{\mathrm{maximum}}$

Table 1 Results of univariate generalized additive models investigating the effects of environmental productivity (estimated by normalised difference vegetation index, NDVI) and its seasonal variation on geographical variation in assemblage mean clutch sizes of South African birds.

	Without taxonomy				Controlled for taxonomy			
Full dataset	Estimated d.f.	Deviance	F	P	Estimated d.f.	Deviance	F	P
$\mathrm{NDVI}_{\mathrm{maximum}}$*	2	17.7	199.8	< 0.001	6.2	11.1	31.1	< 0.001
$\mathrm{NDVI}_{\mathrm{seasonality}}$†	3.9	4.6	21.4	< 0.001	5.7	17.2	63.4	< 0.001
RES1‡	7.9	24.7	68.9	< 0.001	8.3	9.1	20.6	< 0.001
RES2§	8.2	20.6	54.1	< 0.001	6.8	11.4	33.4	< 0.001
Subset								
$\mathrm{NDVI}_{\mathrm{maximum}}$*	4.6	28.3	57.0	< 0.001	1	5.6	42.4	< 0.001
$\mathrm{NDVI}_{\mathrm{seasonality}}$†	3.9	26.8	12.9	< 0.001	2.9	31.6	26.5	< 0.001

*$\mathrm{NDVI}_{\mathrm{maximum}}$, average maximum monthly NDVI.
†$\mathrm{NDVI}_{\mathrm{seasonality}}$, seasonality in NDVI.
‡RES1, residuals from ordinary least square regression between $\mathrm{NDVI}_{\mathrm{maximum}}$ (response variable) and $\mathrm{NDVI}_{\mathrm{seasonality}}$ (explanatory variable).
§RES2, residuals from ordinary least square regression between $\mathrm{NDVI}_{\mathrm{seasonality}}$ (response variable) and $\mathrm{NDVI}_{\mathrm{maximum}}$ (explanatory variable).

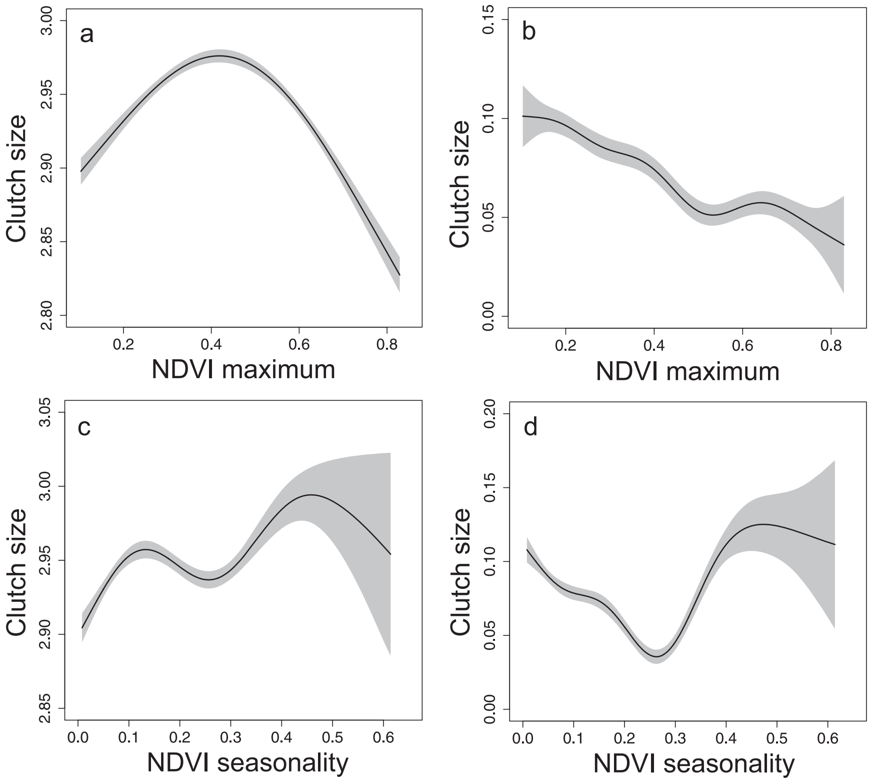


Figure 4 Nonlinear relationships (fitted by generalized additive models) between assemblage mean clutch size of South African passerines, maximum normalized difference vegetation index (NDVI) (a, b), and seasonality in NDVI (the difference between minimum and maximum NDVI (c, d). Raw clutch size data (a, c) and clutch size data controlled for taxonomy (b, d) are provided. Grey areas indicate confidence intervals.

(Fig. 4a). After controlling for taxonomy, the effect of NDVI$_{\text{maximum}}$ was significant ($F = 31.07$, $P < 0.001$, estimated d.f. = 6.18, 11.1% of variation explained). No model simplification was justified. Clutch size decreased nonlinearly with increasing NDVI$_{\text{maximum}}$ (Fig. 4b).

Further, we found a significant effect of NDVI$_{\text{seasonality}}$ on clutch size ($F = 12.14$, $P < 0.001$, estimated d.f. = 6.08, 4.8% of deviance explained). Simplification (upper limit of d.f.s set to five) caused no significant change in the model deviance ($F = 2.06$, $P = 0.12$). This simplified model explained 4.6% of the deviance ($F = 21.4$, $P < 0.001$, estimated d.f. = 3.94) and revealed a nonlinearly increasing relationship between clutch size and NDVI$_{\text{seasonality}}$ (Fig. 4c). After controlling for taxonomy, the effect of NDVI$_{\text{seasonality}}$ was still significant ($F = 47.18$, $P < 0.001$, estimated d.f. = 6.97, 17.2% of variation explained). Simplification (upper limit of d.f.s set to seven) caused no significant change in the model deviance ($F = 1.14$, $P = 0.30$). This simplified model explained 17.2% of the deviance ($F = 63.36$, $P < 0.001$, estimated d.f. = 5.7) and revealed a reverse hump-shaped relationship between clutch size and NDVI$_{\text{seasonality}}$ (Fig. 4d).

Residual analyses

We further investigated the relationships between clutch size and RES1 and RES2, respectively (Table 1). Clutch size decreased nonlinearly with increasing RES1 ($F = 68.89$, $P < 0.001$, estimated d.f. = 7.88; Fig. 5a) and explained 24.7% of the variance. No model reduction was justified. After controlling for taxonomy the model was still significant ($F = 20.56$, $P < 0.001$, estimated d.f. = 8.34) and explained 9.1% of the variance (Fig. 5b). No model reduction was justified. Then we investigated the relationship between clutch size and RES2. The model revealed a nonlinear and positive relationship ($F = 54.11$, $P < 0.001$, estimated d.f. = 8.18; Fig. 5c) and the model explained 20.6% of the total variance. No model reduction was justified. After controlling for taxonomy, RES2 explained less variance in clutch size (11.5%) but the model was still significant ($F = 26.41$, $P < 0.001$, estimated d.f. = 8.00). Simplification (upper limit of d.f.s set to eight) caused no significant change in the model deviance ($F = 2.10$, $P = 0.14$). The simplified model explained 11.4% of the variance ($F = 33.35$, $P < 0.001$, estimated d.f. = 6.78; Fig. 5d).

Subset analyses

Using subsetted dataset (see above), we limited variation in NDVI$_{\text{seasonality}}$ and tested the effect of NDVI$_{\text{maximum}}$ on variation in clutch size (Table 1). We found a unimodal but decreasing relationship ($F = 41.96$, $P < 0.001$, estimated d.f. = 5.46). Simplification (upper limit of d.f.s set to six) caused no significant change in the model deviance ($F = 2$, $P = 0.158$). The final model explained 28.3% of the total variation ($F = 57.03$, $P < 0.001$, estimated d.f. = 4.55; Fig. 6a). After we controlled for taxonomy, the relationship changed to linearly decreasing (Fig. 6b) and explained only 5.58% of the variance ($F = 42.35$, $P < 0.001$, estimated d.f. = 1). Using the reversely subsetted dataset (limited variation in NDVI$_{\text{maximum}}$), we tested the effect of NDVI$_{\text{seasonality}}$ on clutch size. We found a nonlinear and positive relationship

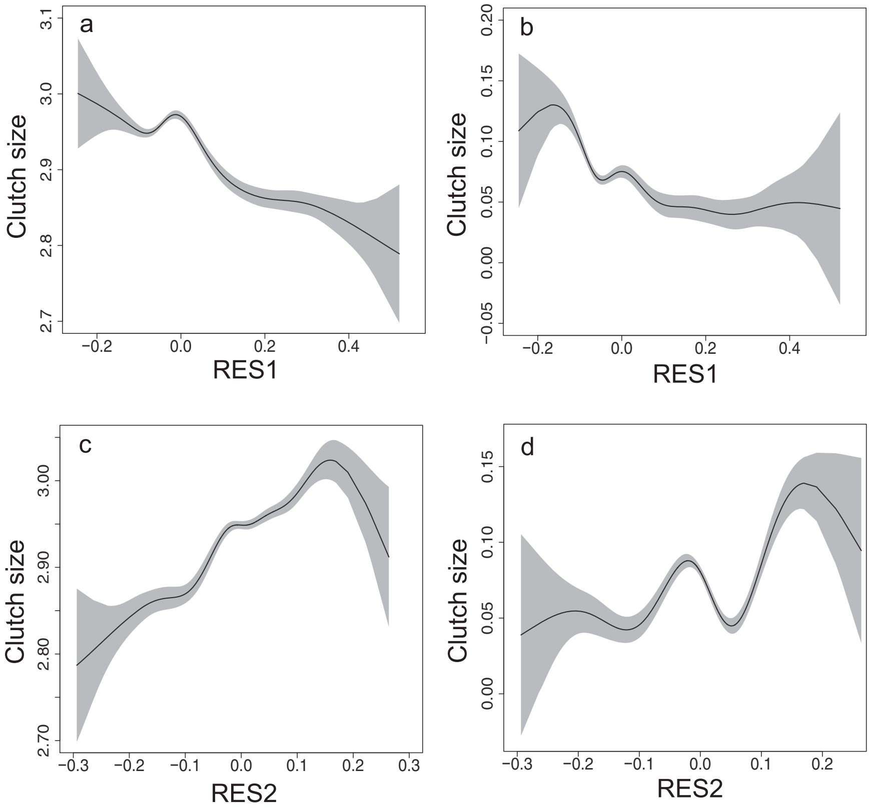


Figure 5 Nonlinear relationships (fitted by generalized additive models) between assemblage mean clutch size of South African passerines and residuals from ordinary least squares regressions between: (1) maximum normalized difference vegetation index (NDVI) as a response variable and the seasonality in NDVI (the difference between minimum and maximum NDVI) as an explanatory variable (RES1; a, b); (2) seasonality in NDVI as a response variable and maximum NDVI as an explanatory variable (RES2; c, d). Raw clutch size data (a, c) and clutch size data controlled for taxonomy (b, d) are provided. Grey areas indicate confidence intervals.

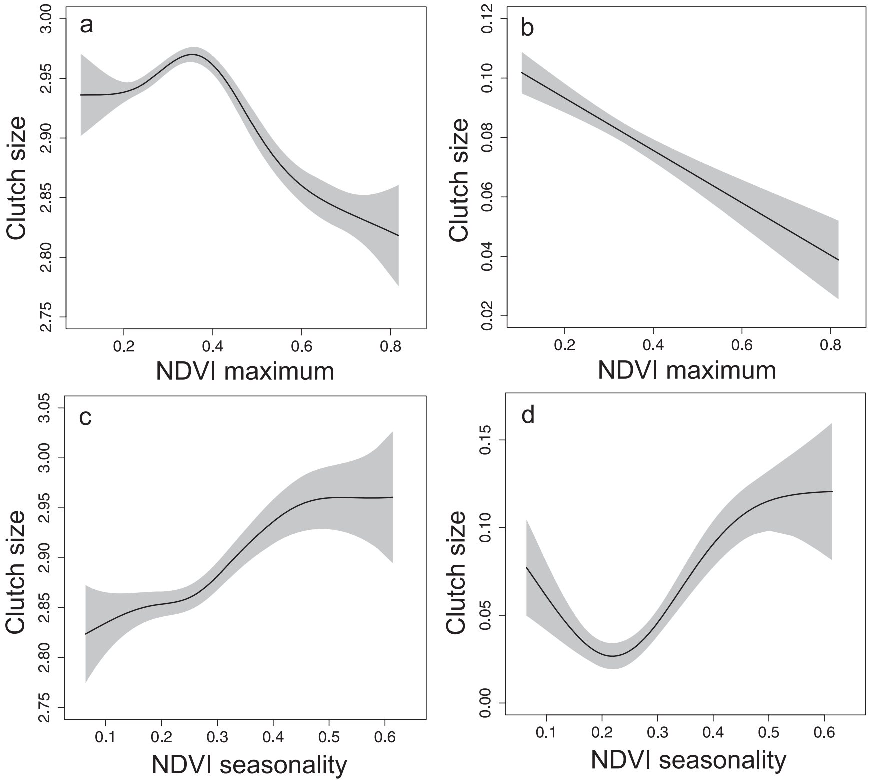


Figure 6 Nonlinear relationships (fitted by generalized additive models) between assemblage mean clutch size of South African passerines and maximum normalized difference vegetation index (NDVI) and NDVI seasonality within selected subsets of the whole dataset (see Methods and Figs 2 & S8). Relationships between assemblage mean clutch size and maximum NDVI for the dataset with restricted variation in NDVI seasonality (a, b). Relationships between assemblage mean clutch size and seasonality in NDVI for the dataset with restricted variation in maximum NDVI (c, d). Raw clutch size data (a, c) and clutch size data controlled for taxonomy (b, d) are provided. Grey areas indicate confidence intervals.

(Fig. 6c) that explained 26.8% of the total variance ($F = 12.86$, $P < 0.001$, estimated d.f. = 3.92). The pattern of the relationship changed to reverse hump-shaped after controlling for taxonomy ($F = 15.76$, $P < 0.001$, estimated d.f. = 4.03). The simplified model (upper limit of d.f.s set to four) did not differ significantly ($F = 1.117$, $P = 0.299$) and explained 31.6% of the variation ($F = 26.45$, $P < 0.001$, estimated d.f. = 2.92; Fig. 6d).

In summary, we found nonlinear patterns in the relationships between environmental variables and clutch size. However, the positive effect of seasonality on clutch size was still detectable in the data and the relationship between maximum productivity and clutch size seemed to be rather unimodal. The inclusion of taxonomy weakened the explanatory power of the environmental variables.

Differences among feeding guilds

The analyses performed within feeding guilds revealed that relationships between clutch size and environmental variables observed in insectivorous and fruit eating birds correspond to the situation observed in all passerines. In contrast, clutch size of granivorous species showed the opposite pattern. It decreased with increasing $\mathrm{NDVI}_{\mathrm{seasonality}}$ and increased with increasing $\mathrm{NDVI}_{\mathrm{maximum}}$. For results see Appendices S3–S5, S9 & S10.

DISCUSSION

Our results highlight the importance of Ashmole's specification (Ashmole, 1963) of the food limitation hypothesis originally proposed by Lack (1947). Assemblage mean clutch size reveals a significant spatial pattern across South African passerine assemblages (Fig. 3). Interestingly, two highly productive regions – the moist grasslands and savanna-woodlands in the eastern parts of South Africa – show consistent but different patterns. Moist grassland passerines lay larger clutches while moist savanna woodland birds lay smaller ones. Although both environments are productive, they differ in seasonality, which is higher in grasslands. This finding provides indirect support for Ashmole's hypothesis.

Using a more rigorous approach, we revealed that the relationship between clutch size and maximum NDVI is hump-shaped, whereas NDVI seasonality had a positive effect on clutch size. In other analyses, we fixed the variation in environmental variables statistically and found that relatively higher levels of maximum NDVI lead to smaller clutches, while relatively higher levels of seasonality in NDVI lead to larger clutches. We obtained similar results when the variation in environmental variables was fixed by subsetting the whole dataset. Seasonal variation in NDVI relative to its overall levels drives the clutch sizes of passerines across South Africa, thus providing a support for Ashmole's hypothesis.

We are obviously not the first to have corroborated the primary suggestion that resource seasonality increases bird clutch size. Lack & Moreau (1965) found smaller passerine clutches in tropical forests than in more seasonal savannas. Convincing evidence was also provided by Ricklefs (1980), who used information about 13 avian assemblages at different latitudes. Jetz *et al.* (2008) showed an important effect of environmental seasonality on avian clutch size at a global scale. However, their analysis revealed the effect of temperature seasonality (estimated as temperature range), not of the ratio characterizing seasonality in resource levels. Ashmole's hypothesis in combination with the cost of reproduction was also supported by simulations performed by Griebeler & Böhning-Gaese (2004). Finally, Lepage & Lloyd (2004) and Hořák *et al.* (2011) reported larger clutches in more seasonal environments for subsets of South African birds. However, here we were able to separate the effect of overall productivity level from seasonality itself, and show that seasonality determines clutch size variation not only between different latitudes but also along longitude and within one biogeographical unit. Moreover, our data confirmed a unique, so far overlooked, prediction of Ashmole's hypothesis: clutch sizes decrease with increasing maximum NDVI at fixed levels of NDVI difference (seasonality), because the same increment of productivity represents a smaller portion of total amount of resources in highly productive environment (see Fig. 1). This *relatively* small difference in resource availability is then reflected by only a low per capita increase in the amount of available food for nestlings.

The relationships described here frequently show nonlinear patterns. This might reflect real patterns (e.g. nonlinear variation in competition for food along an environmental productivity axis; Ballance *et al.*, 1997), but also some confounding effects due to the macroecological approach employed here. Nonlinear relationships could be attributed to other factors related differently to environmental productivity that also affect clutch size, such as nest predation (Skutch, 1949) – though this seems not to be the case here (Hořák *et al.*, 2011) – or life expectancy (Martin, 2002). Alternatively, they might be caused by factors which do not directly influence clutch size but are related to observed clutch size variation, such as geographical distributions of species. At least to some extent, distributional patterns seem to be a result of factors not directly linked to the environment, such as dispersal, stochasticity, evolutionary history or host–pathogen interactions (e.g. Ricklefs, 2013). Therefore, macroecological analyses based on species distributions may contain such kinds of noise.

The geographical pattern in assemblage mean clutch size we describe here seems to be partly caused by the different geographical distribution of passerine families, since it changed when we controlled for the taxonomic membership of birds (Fig. 3b). The relationships between the environment and clutch size thus seem to be driven by the differences in geographical distributions of avian families and phylogenetic conservatism in clutch size rather than by an adaptive variation in a response to the environment within families. However, using subsets of grid cells we found that taxonomical information did not change the observed relationships too much (compare Figs 4 and 5 with Fig. 6), supporting the idea of environmentally induced variation in clutch size even within families. This inconsistency might be related to the differences between the methodological approaches. The subsets of data include only parts of the focal geographical space, i.e. places with extremely high estimates of maximum NDVI and places with extremely low estimates of NDVI seasonality (see Fig. 2). These extreme conditions may provide strong selective pressure on avian variation of clutch size within families. The values of NDVI are highly spatially autocorrelated (see Appendix S7) and thus the selected grid cell subsets contain species sets that more or less belong to the same geographical regions (see Appendix S8). Consequently, our disparate results provide information for different spatial scales. For South Africa as a whole, spatial segregation among families with different clutch sizes plays a role. For the smaller spatial scales that include only smaller regions and therefore contain taxonomically more homogeneous assemblages, even slight differences driven by interspecific variation within families are pronounced.

These issues are related to the fact that our investigations of local assemblages are complicated by spatial autocorrelation (Dormann *et al.*, 2007). For that reason, we also performed analyses in which we controlled for this phenomenon. Especially for subsetted datasets, these analyses provided weaker support for the principal conclusions made here. This suggests that the spatial proximity of avian assemblages lies behind the similarity in clutch sizes of their members, and nearby locations are thus not independent. However, the interpretation of this fact is not straightforward. Since environmental variables reveal similarly strong spatial structure, we might speak rather about ‘spatial dependence’ *sensu* Legendre *et al.* (2002). Consequently, it is almost impossible to disentangle the effect of spatially structured environmental conditions on clutch size variation from spatial autocorrelation of assemblage compositions per se. We found that differential geographical distributions of avian taxa are likely to be responsible for the relationship between clutch size and environment, and it is reasonable to assume that geographical distribution reflects links between environmental conditions and avian adaptations. Therefore, spatial dependence among grid cells in the data does not negate our ecological explanations.

We acknowledge that other mechanisms besides density-dependent food limitation could play a role in explaining clutch size variation among bird assemblages. Specifically, the probability of future reproduction in terms of survival probability (Williams, 1966; Martin, 2002) and the number of reproductive attempts (Moreau, 1944) might be connected to resource levels in the environment and their changes (Erikstad *et al.*, 1998; Orzack & Tuljapurkar, 2001). Higher and/or stable levels of food resources might lower the probability of adult mortality (Oro & Furness, 2002; Harding *et al.*, 2011) and smaller clutches might be expected as a consequence. Also, seasonality influences the length of the bird breeding season, and more breeding attempts may be thus traded off for smaller clutches in less seasonal environments (Slagsvold, 1984; Farnsworth & Simons, 2001). However, in this case there would be no obvious reason for observing the decrease in assemblage mean clutch size with increasing maximum productivity at fixed levels of seasonality. Finally, abundant/diversified predator assemblages might increase nest predation pressure in more productive environments, in which in turn smaller clutches should be observed. This would fit with the patterns described here, although it would not explain the effect of seasonality on clutch size. Also, abundant bird populations and better concealed nests can in fact lower nest predation risk in more complex environments (Hořák *et al.*, 2011), which casts doubts on the generality of this explanation.

We found contrasting patterns for granivorous species (see Appendices S9 & S10). We suggest that this difference is due to the fact that granivore bird populations are not limited during the non-breeding season because the seed bank represents a stable food resource, so that the seasonality effect as described by Ashmole (1963) is not applicable. Granivorous species also feed their nestlings with insects, an additional source of food unrelated to the resource responsible for their population control. Therefore, their clutch size investment might not reflect availability of resources relatively to population sizes, and clutch size variation may rather mirror the absolute amount of available resources in the environment, leading to larger clutches at higher NDVI levels. In more seasonal locations, less food may be left for granivores due to higher breeding synchrony and stronger interspecific competition with insectivores which are better adapted for insect collection. Anyway, the finding that our predictions concerning NDVI and its seasonality do not work for the group whose food resource is apparently unrelated to NDVI is in accord with the other patterns reported here.

In sum, Ashmole’s formulation has enabled application of Lack’s original view to the comparison among different regions (differing in seasonality), thus explaining major geographical trends in assemblage mean clutch size across South Africa. The conclusions made here may be quite general and can potentially be applied to the tropical–extratropical comparison. Indeed, the ‘seasonality hypothesis’ predicts smaller clutches in highly productive but aseasonal tropical environments. We have also shown that geographical patterns in clutch size are most probably formed by both the different geographical distribution of higher taxa and the clutch size variation at the species level within passerine families. To completely understand the importance of seasonality for clutch size evolution, field data on local bird densities should be included to allow more mechanistic models of density-dependent food availability.

ACKNOWLEDGEMENTS

We are grateful to the editors and anonymous reviewers whose comments significantly improved the manuscript. The study was supported by the Czech Science Foundation (project no. P505/11/1617).

REFERENCES

Ashmole, N.P. (1963) The regulation of numbers of tropical oceanic birds. *Ibis*, **103**, 458–473.

Ballance, L.T., Pitman, R.L. & Reilly, S.B. (1997) Seabird community structure along a productivity gradient: importance of competition and energetic constraint. *Ecology*, **78**, 1502–1518.

Chong, D.L.S., Mougin, E. & Gastellu-Etchegorry, J.P. (1993) Relating the global vegetation index to net primary productivity and actual evapotranspiration over Africa. *Remote Sensing*, **14**, 1517–1546.

Crawley, M.J. (2007) *The R book*. John Wiley & Sons Ltd, Chichester.

Dormann, C.F., McPherson, J.M., Araújo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Daniel Kissling, W., Kühn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schröder, B., Schurr, F.M. & Wilson, R. (2007) Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography*, **30**, 609–628.

Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G., Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E., Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D. & Lautenbach, S. (2013) Collinearity: a review of methods to deal with it and a simulation study evaluating their performance. *Ecography*, **36**, 027–046.

Erikstad, K.E., Fauchald, P., Tveraa, T. & Steen, H. (1998) On the cost of reproduction in long-lived birds: the influence of environmental variability. *Ecology*, **79**, 1781–1788.

Farnsworth, G.L. & Simons, T.R. (2001) How many baskets? Clutch sizes that maximize annual fecundity of multiple-brooded birds. *The Auk*, **118**, 973–982.

Gordo, O. (2007) Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Climate Research*, **35**, 37–58.

Goward, S.N. & Dye, D.G. (1987) Evaluating North American net primary productivity with satellite observations. *Advances in Space Research*, **7**, 165–174.

Griebeler, E.M. & Böhning-Gaese, K. (2004) Evolution of clutch size along latitudinal gradients: revisiting Ashmole's hypothesis. *Evolutionary Ecology Research*, **6**, 679–694.

Harding, A.A., Welcker, J., Steen, H., Hamer, K.C., Kitaysky, A.S., Fort, J., Talbot, S.L., Cornick, L.A., Karnovsky, N.J., Gabrielsen, G.W. & Grémillet, D.W. (2011) Adverse foraging conditions may impact body mass and survival of a high Arctic seabird. *Oecologia*, **167**, 49–59.

Harrison, J.A., Allan, D.G., Underhill, L.G., Herremans, M., Tree, A.J., Parker, V. & Brown, C.J. (eds) (1997) *The atlas of southern African birds. Vol. 2: passerines*. BirdLife South Africa, Johannesburg.

Hockey, P.A.R., Dean, W.R.J. & Ryan, P.G. (eds) (2005) *Roberts birds of southern Africa*, 7th edn. Trustees of the John Voelcker Bird Book Fund, Cape Town.

Hořák, D., Sedláček, O., Tószögyová, A., Albrecht, T., Ferenc, M., Jelínek, V. & Storch, D. (2011) Geographic variation in avian clutch size and nest predation risk along a productivity gradient in South Africa. *Ostrich*, **82**, 175–183.

Jetz, W., Sekercioglu, C.H. & Böhning-Gaese, K. (2008) The worldwide variation in avian clutch size across species and space. *PLoS Biology*, **6**, 12, e303.

Koenig, W.D. (1984) Geographic variation in clutch size in the northern flicker (*Colaptes auratus*) – support for Ashmole's hypothesis. *The Auk*, **101**, 698–706.

Lack, D. (1947) The significance of clutch-size. *Ibis*, **89**, 668–668.

Lack, D. (1948) The significance of clutch-size. 3. Some interspecific comparisons. *Ibis*, **90**, 1, 25–45.

Lack, D. & Moreau, R.E. (1965) Clutch-size in tropical passerine birds of forest and savanna. *Oiseau*, **35**, 76–89.

Lafage, D., Secondi, J., Georges, A., Bouzillé, J.-B. & Pétillon, J. (2014) Satellite-derived vegetation indices as surrogate of species richness and abundance of ground beetles in temperate floodplains. *Insect Conservation and Diversity*, **7**, 327–333.

Lassau, S.A. & Hochuli, D.F. (2008) Testing predictions of beetle community patterns derived empirically using remote sensing. *Diversity and Distributions*, **14**, 138–147.

Legendre, P., Dale, M.R.T., Fortin, M.-J., Gurevitch, J., Hohn, M. & Myers, D. (2002) The consequences of spatial structure for the design and analysis of ecological field surveys. *Ecography*, **25**, 601–615.

Lepage, D. & Lloyd, P. (2004) Avian clutch size in relation to rainfall seasonality and stochasticity along an aridity gradient across South Africa. *Ostrich*, **75**, 259–268.

Martin, T.E. (2002) A new view of avian life history evolution tested on incubation paradox. *Proceedings of the Royal Society B: Biological Sciences*, **269**, 309–316.

Moreau, R.E. (1944) Clutch-size: a comparative study, with special reference to African birds. *Ibis*, **86**, 286–347.

Oro, D. & Furness, R.W. (2002) Influences of food availability and predation on survival of kittiwakes. *Ecology*, **83**, 2516–2528.

Orzack, S.H. & Tuljapurkar, S. (2001) Reproductive effort in variable environments, or environmental variation is for the birds. *Ecology*, **82**, 2659–2665.

Paruelo, J.M., Epstein, H.E., Lauenroth, W.K. & Burke, I.C. (1997) ANPP estimates from NDVI for the central grassland region of the United States. *Ecology*, **78**, 953–958.

Patten, M.A. (2007) Geographic variation in calcium and clutch size. *Journal of Avian Biology*, **38**, 637–643.

R Development Core Team (2013) *R: a language and environment for statistical computing*. R Foundation for Statistical Computing, Vienna.

Rangel, T.F., Diniz-Filho, J.A.F. & Bini, L.M. (2010) SAM: a comprehensive application for spatial analysis in macroecology. *Ecography*, **33**, 46–50.

Ricklefs, R.E. (1980) Geographical variation in clutch size among passerine birds – Ashmole's hypothesis. *The Auk*, **97**, 38–49.

Ricklefs, R.E. (2013) Habitat-independent spatial structure in populations of some forest birds in eastern North America. *Journal of Animal Ecology*, **82**, 145–154.

Schmidt, H. & Karnieli, A. (2002) Analysis of the temporal and spatial vegetation patterns in a semi-arid environment observed by NOAA AVHRR imagery and spectral ground measurements. *International Journal of Remote Sensing*, **23**, 3971–3990.

Skutch, A.F. (1949) Do tropical birds rear as many young as they can nourish. *Ibis*, **91**, 430–458.

Slagsvold, T. (1975) Hypotheses on breeding time and clutch-size in birds. *Norwegian Journal of Zoology*, **23**, 219–222.

Slagsvold, T. (1984) Clutch size variation of birds in relation to nest predation: on the cost of reproduction. *Journal of Animal Ecology*, **53**, 945–953.

Williams, G.C. (1966) Natural selection, the cost of reproduction, and a refinement of Lack's principle. *The American Naturalist*, **100**, 687–690.

SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1 Results of linear models.
Appendix S2 Results of generalized least squares models.
Appendix S3 Results of ordinary least squares models for particular feeding guilds.
Appendix S4 Results of spatial generalized least squares models for particular feeding guilds.
Appendix S5 Results of generalized additive models for particular feeding guilds.
Appendix S6 Effect of the presence of intra-African migrants in local assemblages on assemblage mean clutch size spatial patterns.
Appendix S7 Geographical variation in normalized difference vegetation index variables.
Appendix S8 Geographical locations of grid cell subsets used in the analyses.
Appendix S9 Differences in geographical patterns of assemblage mean clutch size among the three feeding guilds.
Appendix S10 Differences in nonlinear relationships between assemblage mean clutch size and normalized difference vegetation index variables among the three feeding guilds.

BIOSKETCHES

David Hořák is an assistant professor at Charles University in Prague who focuses his research on the ecology and biogeography of birds in Africa and Europe. He is especially interested in functional aspects of biodiversity and their links to species richness.

Anna Tószögyová is a PhD student at Charles University. She is interested in biogeography topics and spatial statistics. Her research is focused on African avifauna.

David Storch is a professor at Charles University. He is interested in macroecology, evolutionary ecology and biogeography, with particular emphasis on diversity patterns and spatial scaling.

Editor: Karl Evans

Appendix S1. Results of Linear models evaluating the effect of NDVI$_{\text{maximum}}$ and NDVI$_{\text{seasonality}}$ (maximum and seasonality in normalised difference vegetation index, see the main text) on assemblage mean clutch size of South African passerines.

In the first step, we fitted a simple linear model evaluating the effect of NDVI$_{\text{maximum}}$, NDVI$_{\text{seasonality}}$ and their interaction on clutch size. The model was highly significant ($F = 245.8$, $p < 0.001$, Δ Df = 3) and explained 28.5 % of the variation in the data. NDVI$_{\text{maximum}}$ was related significantly and negatively ($F = 51.5$, $p < 0.001$, Δ Df = 1) to clutch size, while NDVI$_{\text{seasonality}}$ was related significantly and positively to clutch size ($F = 468.2$, $p < 0.001$, Δ Df = 1). However, the model also revealed a negative and significant interaction between NDVI$_{\text{maximum}}$ and NDVI$_{\text{seasonality}}$ ($F = 217.7$, $p < 0.001$, Δ Df = 1). We achieved slightly different results when we used information about clutch sizes controlled for the effect of taxonomy (see Methods). The model was still significant ($F = 88.2$, $p < 0.001$, Δ Df = 3) but explained less variation in the data (12.5 %). NDVI$_{\text{maximum}}$ was significantly and negatively related to clutch size ($F = 207.0$, $p < 0.001$, Δ Df = 1), and similarly, we found a significant and negative effect of NDVI$_{\text{seasonality}}$ ($F = 12.25$, $p < 0.001$, Δ Df = 1). We also found a significant but positive interaction between NDVI$_{\text{maximum}}$ and NDVI$_{\text{seasonality}}$ ($F = 45.4$, $p < 0.001$, Δ Df = 1).

Given the significant interactions in the models above, we decided to perform univariate linear models explaining separately the variation in clutch size by NDVI$_{\text{maximum}}$ and NDVI$_{\text{seasonality}}$, respectively. NDVI$_{\text{maximum}}$ was related negatively to clutch size (the trend retained even after controlling for taxonomy) and NDVI$_{\text{seasonality}}$ was related positively to clutch size (but we observed the reverse trend when controlling for taxonomy). Even though all the relationships were significant (all $p < 0.001$), environmental variables explained only a rather low proportion of the variation in clutch size (up to 10%); for details see Table S1.

Residual analyses

We next tried to explain the variation in clutch size by RES1 in a simple linear model, and found a significant but negative relationship ($F = 422.5$, $p < 0.001$, Δ Df = 1) that explained 18.5% of the total variance. This suggests that within a statistically fixed level of NDVI$_{\text{seasonality}}$, clutch sizes tend to decrease with increasing NDVI$_{\text{maximum}}$. We repeated the analysis using clutch size information controlled for the effect of taxonomy. The model with RES1 as an explanatory variable was statistically significant ($F = 112.4$, $p < 0.001$, Δ Df = 1) and revealed a negative relationship between variables, explaining 5.7% of the total variance. When exploring variation in clutch size by RES2 in a linear model, we found a significant positive relationship ($F = 409.2$, $p < 0.001$, Δ Df = 1) explaining 18.1 % of the total variance. This suggests that within a statistically fixed level of NDVI$_{\text{maximum}}$, clutch sizes tend to increase with increasing NDVI$_{\text{seasonality}}$. After controlling for taxonomy the model with RES2 as an explanatory variable was still positive and significant ($F = 10.8$, $p = 0.001$, Δ Df = 1) but explained only a negligible amount of the total variation (Table S1).

Subset analyses

Using subsetted data (see Methods) we tested the effect of NDVI$_{\text{maximum}}$ on the variation in clutch size. We again found it to be significant and negative ($F = 100.4$, $p < 0.001$, Δ Df =

1), explaining 12.3% of the variation. The relationship remained unchanged after controlling for taxonomy (F = 42.4, p < 0.001, Δ Df = 1), but was weaker (explaining 5.6% of the variance). Second, we subsetted the full dataset reversely by selecting grid cells that had limited variation in $NDVI_{maximum}$ and with this subsample we tested the effect of $NDVI_{seasonality}$ on variation in clutch size. It had a significant and positive effect (F = 54.2, p < 0.001, Δ Df = 1) and the relationship explained 23.2% of the total variance. After controlling for taxonomy, the relationship remained unchanged (F = 41.2, p < 0.001, Δ Df = 1) but $NDVI_{seasonality}$ explained less variation in clutch size (18.8%). It follows from these results that after controlling for maximum productivity the clutch size increases with increasing seasonality. When seasonality is fixed, clutch size decreases with productivity. The patterns are weaker when controlling for taxonomy, since a significant proportion of clutch size variation can be observed among families.

Table S1. Results of univariate linear models investigating the effects of environmental productivity (estimated by NDVI – Normalized Difference Vegetation Index) and its seasonal variation on geographical variation in assemblage mean clutch sizes of South African birds.

	Without taxonomy				Controlled for taxonomy			
Full dataset	Estimate (se)	R^2	F	P	Estimate (se)	R^2	F	p
NDVI $_{\text{maximum}}$[*]	-0.056 (0.009)	0.02	37.6	< 0.001	-0.094 (0.007)	0.10	200.9	< 0.001
NDVI $_{\text{seasonality}}$[†]	0.080 (0.015)	0.02	28.5	< 0.001	-0.107 (0.011)	0.05	90.3	< 0.001
RES1[‡]	-0.301 (0.015)	0.19	422.5	< 0.001	-0.128 (0.012)	0.06	112.4	< 0.001
RES2[§]	0.491 (0.024)	0.18	409.2	< 0.001	0.067 (0.020)	0.01	10.8	< 0.01
Subset								
NDVI $_{\text{maximum}}$[*]	-0.174 (0.017)	0.12	100.4	< 0.001	-0.088 (0.014)	0.06	42.4	< 0.001
NDVI $_{\text{seasonality}}$[†]	0.324 (0.045)	0.23	54.2	< 0.001	0.199 (0.031)	0.19	41.6	< 0.001

[*] NDVI $_{\text{maximum}}$ – average maximum monthly NDVI

[†] NDVI $_{\text{seasonality}}$ – seasonality in NDVI

[‡] RES1 – residuals from OLS regression between NDVI $_{\text{maximum}}$ (response variable) and NDVI $_{\text{seasonality}}$ (explanatory variable)

[§] RES2 – residuals from OLS regression between NDVI $_{\text{seasonality}}$ (response variable) and NDVI $_{\text{maximum}}$ (explanatory variable)

Appendix S2. Results of univariate spatial GLS models investigating effects of environmental productivity (estimated by NDVI – normalized difference vegetation index) and its seasonal variation on geographical variation in assemblage mean clutch sizes of South African birds. R^2 indicates variance explained by predictor variable (exluding space).

	Without taxonomy				Controlled for taxonomy			
Full dataset	Std Coeff (se)	R^2	t	P	Std Coeff (se)	R^2	t	P
$\mathrm{NDVI}_{\mathrm{maximum}}$[*]	-0.172 (0.024)	0.02	-2.88	0.004	-0.078 (0.015)	0.04	-1.58	0.114
$\mathrm{NDVI}_{\mathrm{seasonality}}$[†]	0.098 (0.031)	0.01	2.05	0.041	0.028 (0.019)	0.00	0.74	0.462
RES1[‡]	-0.176 (0.023)	0.12	-5.38	< 0.001	-0.062 (0.014)	0.03	-2.29	0.022
RES2[§]	0.146 (0.034)	0.10	4.92	< 0.001	0.049 (0.022)	0.01	1.99	0.047
Subset								
$\mathrm{NDVI}_{\mathrm{maximum}}$[*]	-0.141 (0.033)	0.08	-2.14	0.033	-0.138 (0.020)	0.05	-2.56	0.011
$\mathrm{NDVI}_{\mathrm{seasonality}}$[†]	0.197 (0.177)	0.15	0.75	0.454	0.000 (0.352)	0.00	0.00	0.999

[*] $\mathrm{NDVI}_{\mathrm{maximum}}$ – average maximum monthly NDVI

[†] $\mathrm{NDVI}_{\mathrm{seasonality}}$ – seasonality in NDVI

[‡] RES1 – residuals from OLS regression between $\mathrm{NDVI}_{\mathrm{maximum}}$ (response variable) and $\mathrm{NDVI}_{\mathrm{seasonality}}$ (explanatory variable)

[§] RES2 – residuals from OLS regression between $\mathrm{NDVI}_{\mathrm{seasonality}}$ (response variable) and $\mathrm{NDVI}_{\mathrm{maximum}}$ (explanatory variable)

Appendix S3. Results of ordinary least square models investigating effects of environmental productivity (estimated by NDVI – normalized difference vegetation index) and its seasonal variation on geographical variation in assemblage mean clutch sizes among feeding guilds of South African birds. R^2 indicates variance explained by predictor variable.

Full dataset	Insectivores				Frugivores				Granivores			
	Estimate (se)	R^2	F	P	Estimate (se)	R^2	F	P	Estimate (se)	R^2	F	P
General model		0.30	258.9			0.36	350.8			0.56	784.7	
$\text{NDVI}_{\text{maximum}}^{*}$	-0.358 (0.02)			<0.001	-0.851 (0.04)			<0.001	0.896 (0.03)			<0.001
$\text{NDVI}_{\text{seasonality}}^{\dagger}$	1.116 (0.07)			<0.001	0.676 (0.12)			<0.001	0.011 (0.10)			0.914
$\text{NDVI}_{\text{maximum}}*\text{NDVI}_{\text{seasonality}}^{\dagger}$	-0.992 (0.11)			<0.001	0.041 (0.20)			0.834	-0.657 (0.16)			<0.001
Univariate models												
$\text{NDVI}_{\text{maximum}}^{*}$	-0.175 (0.01)	0.12	258.4	<0.001	-0.498 (0.02)	0.29	774.7	<0.001	0.653 (0.01)	0.54	2147	<0.001
$\text{NDVI}_{\text{seasonality}}^{\dagger}$	-0.06 (0.02)	0.01	10.6	<0.01	-0.457 (0.03)	0.09	185.9	<0.001	0.776 (0.03)	0.28	714.5	<0.001
RES1[‡]	-0.453 (0.02)	0.26	652	<0.001	-0.847 (0.03)	0.27	690.1	<0.001	0.833 (0.03)	0.28	712.5	<0.001
RES2[§]	0.556 (0.03)	0.14	310.8	<0.001	0.699 (0.06)	0.07	134.6	<0.001	-0.361 (0.06)	0.02	36	<0.001
Subset												
$\text{NDVI}_{\text{maximum}}^{*}$	-0.302 (0.02)	0.20	176.2	<0.001	-0.587 (0.04)	0.28	272.6	<0.001	0.677 (0.03)	0.39	461.2	<0.001
$\text{NDVI}_{\text{seasonality}}^{\dagger}$	0.401 (0.04)	0.29	73.3	<0.001	0.719 (0.09)	0.27	68.2	<0.001	-0.594 (0.08)	0.25	59	<0.001

[*] $\text{NDVI}_{\text{maximum}}$ – average maximum monthly NDVI

[†] $\text{NDVI}_{\text{seasonality}}$ – seasonality in NDVI

[‡] RES1 – residuals from OLS regression between $\text{NDVI}_{\text{maximum}}$ (response variable) and $\text{NDVI}_{\text{seasonality}}$ (explanatory variable)

[§] RES2 – residuals from OLS regression between $\text{NDVI}_{\text{seasonality}}$ (response variable) and $\text{NDVI}_{\text{maximum}}$ (explanatory variable)

Appendix S4. Results of spatial generalized least square models investigating effects of environmental productivity (estimated by NDVI – normalized difference vegetation index) and its seasonal variation on geographical variation in assemblage mean clutch sizes among feeding guilds of South African birds. R^2 indicates variance explained by predictor variable (excluding space).

Full dataset	Insectivores				Frugivores				Granivores			
	Std Coeff (se)	t	R^2	P	Std Coeff (se)	t	R^2	P	Std Coeff (se)	t	R^2	P
General model			18.1				20.1				31.5	
NDVI$_{\text{maximum}}$[*]	-0.283 (0.049)	-2.87		0.004	-0.258 (0.072)	-3.31		<0.001	0.397 (0.067)	5.31		<0.001
NDVI$_{\text{seasonality}}$[†]	0.593 (0.162)	3.02		0.003	0.073 (0.235)	0.47		0.64	-0.100 (0.219)	-0.67		0.50
NDVI$_{\text{maximum}}$[*] NDVI$_{\text{seasonality}}$[†]	-0.348 (0.235)	-1.71		0.087	-0.014 (0.341)	-0.09		0.93	-0.082 (0.318)	-0.53		0.60
Univariate models												
NDVI$_{\text{maximum}}$[*]	-0.185 (0.037)	-2.47	9.5	0.014	-0.222 (0.054)	-3.78	19.2	0	0.264 (0.05)	4.67	31.7	0
NDVI$_{\text{seasonality}}$[†]	0.130 (0.048)	2.31	0	0.021	-0.042 (0.07)	-0.92	2.4	0.36	-0.026 (0.065)	-0.60	0	0.55
RES1[‡]	-0.196 (0.036)	-4.82	16.2	<0.001	-0.087 (0.053)	-2.7	8.3	0.007	0.160 (0.049)	5.17	14.3	<0.001
RES2[§]	0.167 (0.055)	4.48	9.9	<0.001	0.050 (0.08)	1.7	2.4	0.088	-0.117 (0.074)	-4.10	1.9	<0.001
Subset												
NDVI$_{\text{maximum}}$[*]	-0.327 (0.04)	-5.70	18.4	<0.001	-0.292 (0.059)	-5.10	22.1	0	0.419 (0.063)	7.21	34.9	<0.001
NDVI$_{\text{seasonality}}$[†]	0.198 (0.055)	2.66	17.4	0.008	0.181 (0.104)	2.38	15.7	0.018	-0.331 (0.089)	-4.43	21.9	<0.001

[*] NDVI$_{\text{maximum}}$ – average maximum monthly NDVI

[†] NDVI$_{\text{seasonality}}$ – seasonality in NDVI

[‡] RES1 – residuals from OLS regression between NDVI$_{\text{maximum}}$ (response variable) and NDVI$_{\text{seasonality}}$ (explanatory variable)

[§] RES2 – residuals from OLS regression between NDVI$_{\text{seasonality}}$ (response variable) and NDVI$_{\text{maximum}}$ (explanatory variable)

Appendix S5. Results of generalized additive models investigating the effects of environmental productivity (estimated by NDVI – normalized difference vegetation index) and its seasonal variation on geographical variation in assemblage mean clutch sizes among feeding guilds of South African birds.

Full dataset	Insectivorous				Frugivorous				Granivorous			
	Estimated Df	Dev	F	P	Estimated Df	Dev	F	P	Estimated Df	Dev	F	P
NDVI$_{\text{maximum}}$[*]	2.9	19.1	147	<0.001	2.6	29.9	238.9	<0.001	7.2	54.3	266	<0.001
NDVI$_{\text{seasonality}}$[†]	6.4	4.41	10.6	<0.001	6.5	18.9	55.5	<0.001	6.8	37.3	138.8	<0.001
NDVI$_{\text{maximum}}$ *NDVI$_{\text{seasonality}}$	21.3	34.1	36.2	<0.001	22.2	42	49.7	<0.001	21.1	58.7	101.5	<0.001
RES1[‡]	4.7	27.2	116.4	<0.001	8.2	30.3	90.7	<0.001	5.9	32.4	148.3	<0.001
RES2[§]	5.9	20.3	78.2	<0.001	8.5	20.1	51.1	<0.001	8.7	25	68	<0.001
Subset												
NDVI$_{\text{maximum}}$[*]	4.18	23	40.4	<0.001	4.6	29.1	50.8	<0.001	1.5	39.3	265.9	<0.001
NDVI$_{\text{seasonality}}$[†]	3.65	33.7	19.2	<0.001	3.6	35.5	21.0	<0.001	3.5	30.9	17.7	<0.001

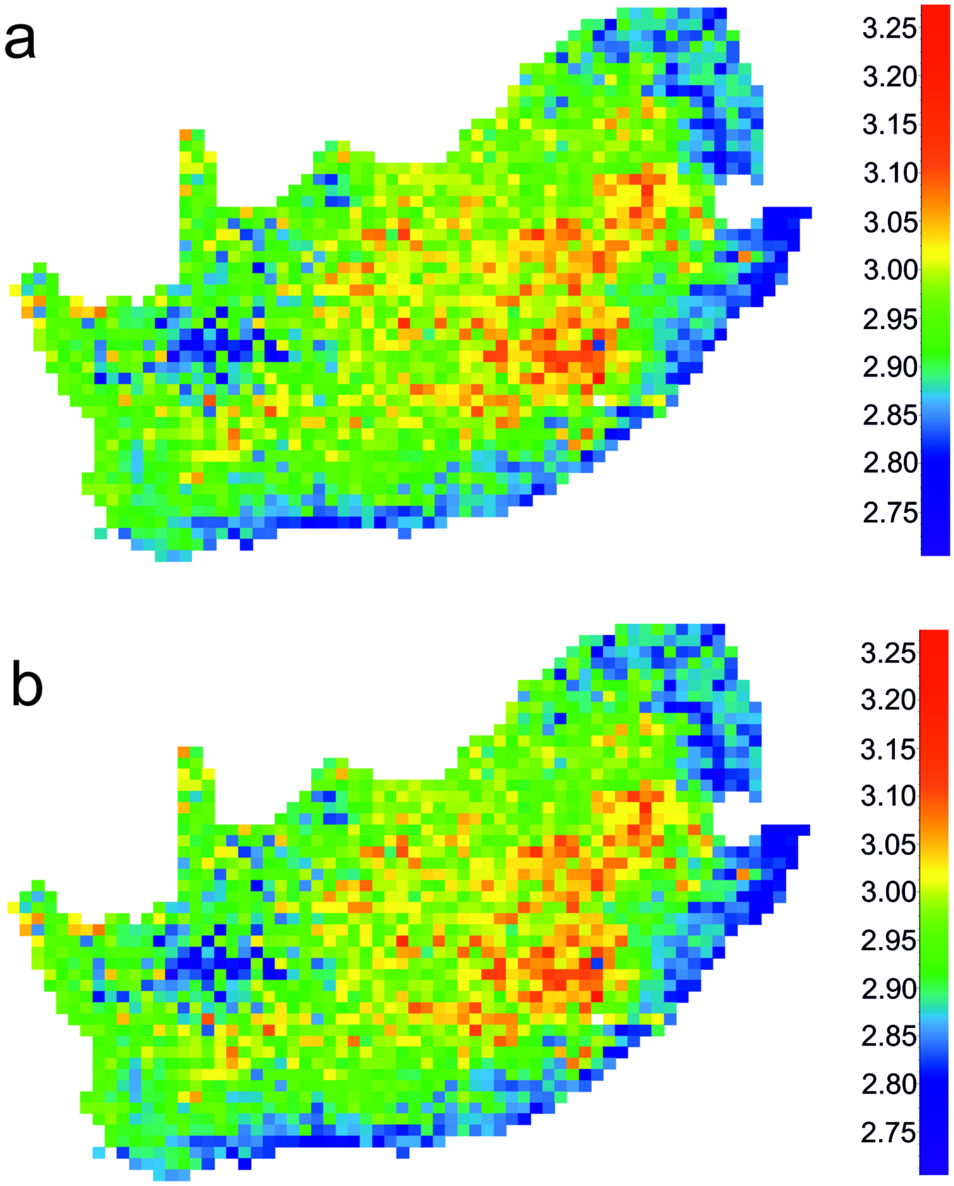
[*] NDVI$_{\text{maximum}}$ – average maximum monthly NDVI

[†] NDVI$_{\text{seasonality}}$ – seasonality in NDVI

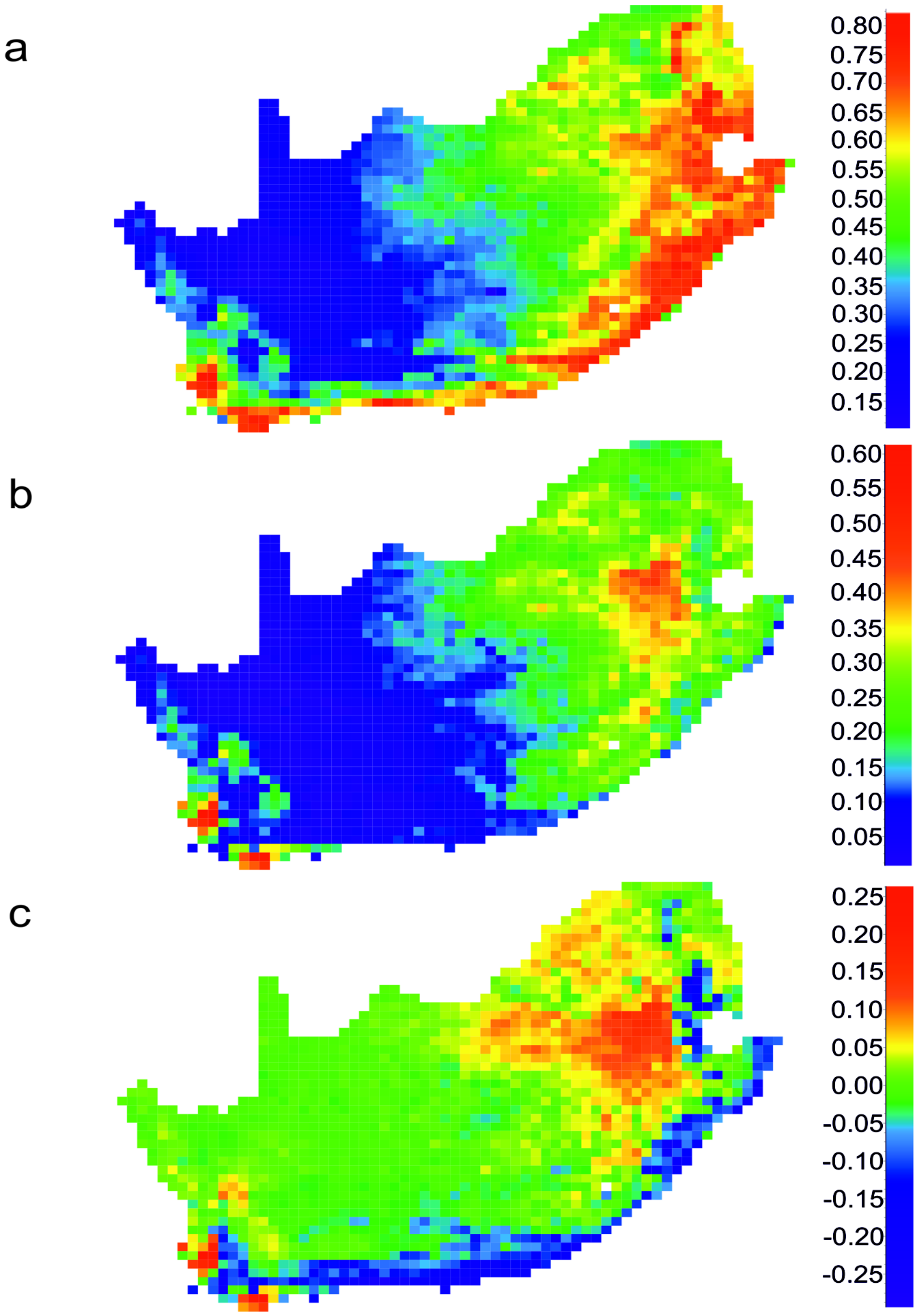
[‡] RES1 – residuals from OLS regression between NDVI$_{\text{maximum}}$ (response variable) and NDVI$_{\text{seasonality}}$ (explanatory variable)

[§] RES2 – residuals from OLS regression between NDVI$_{\text{seasonality}}$ (response variable) and NDVI$_{\text{maximum}}$ (explanatory variable)

Appendix S6. Spatial patterns in assemblage mean clutch size of South African Passerines do not differ between situations when intra-African migrants are (**a**) and are not (**b**) included in the local assemblages.

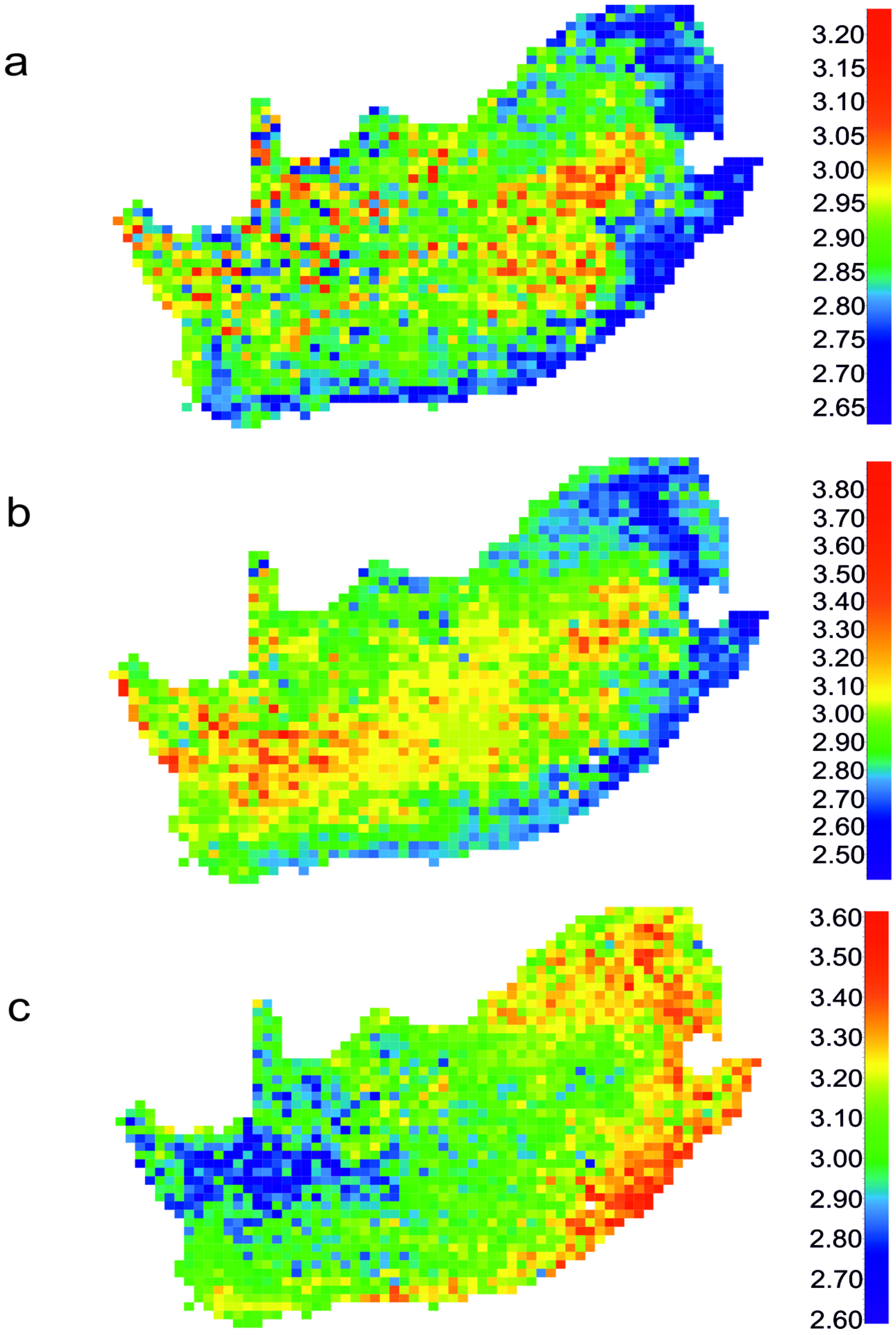


Appendix S7. Geographic variation in maximum NDVI (normalized difference vegetation index; mean from the period 1982-2004) for a month showing the highest value (**a**), and the seasonality in NDVI (absolute difference between maximum and minimum value) (**b**). The residuals from the relationship between seasonality in NDVI as a response variable and the maximum NDVI as an explanatory variable (RES2 see main text) (**c**) in South Africa.

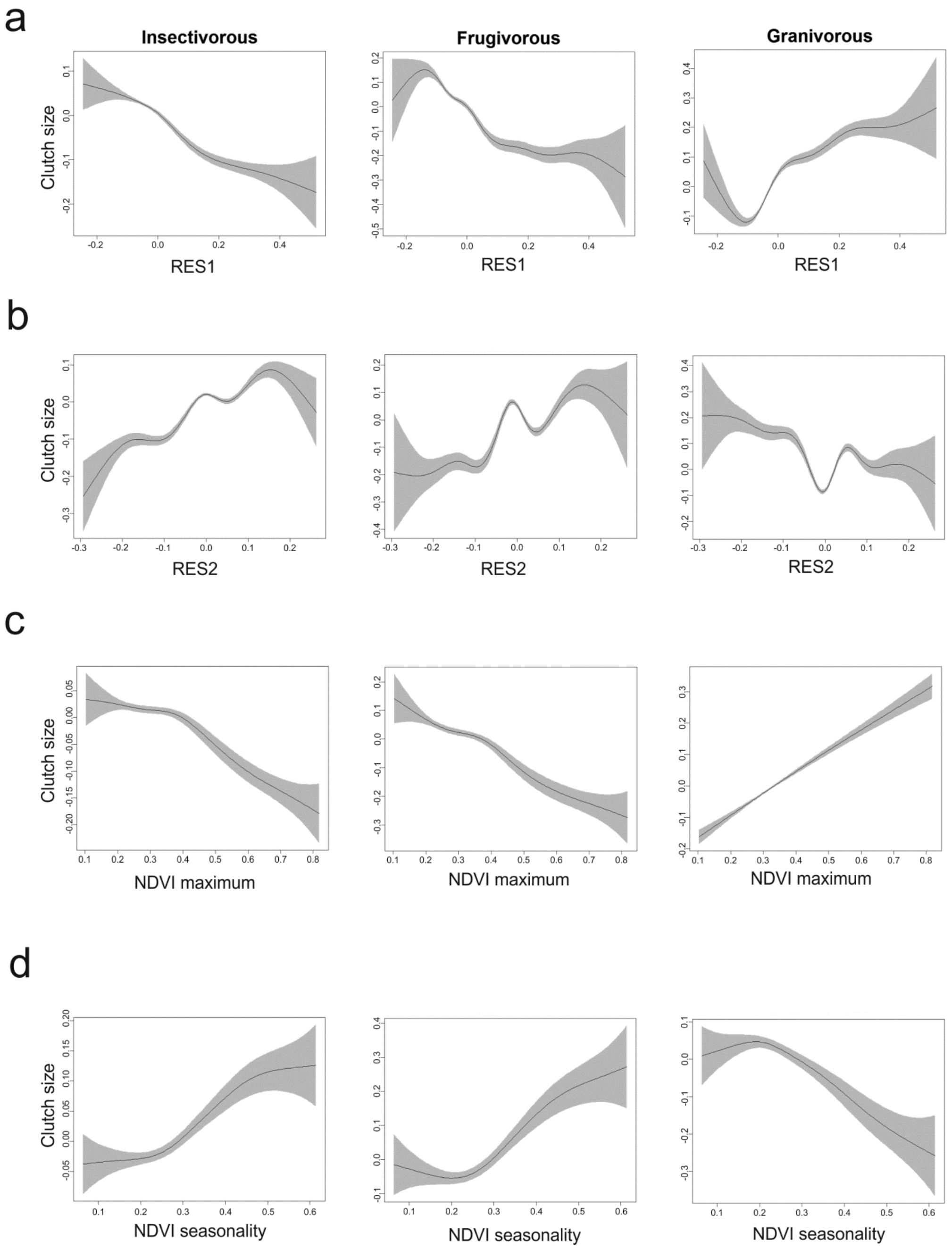


Appendix S8. Geographic locations of grid cells subsets selected so that the variation in maximum NDVI (normalised difference vegetation index) was restricted (**a**), and variation in NDVI seasonality was restricted (**b**). See Methods section for details.

Appendix S9. Geographic variation in assemblage mean clutch sizes of insectivorous passerines (**a**), frugivorous passerines (fruit eating species and species combining fruits and insects in the diet) (**b**), and granivorous passerines (seed eating species and species combining seeds and insects in the diet) (**c**).



Appendix S10. Among guild differences in nonlinear relationships (fitted by Generalized Additive Models) between assemblage mean clutch size of South African passerines and (i) residuals from OLS (ordinary least square) regressions between maximum NDVI (normalised difference vegetation index) as a response variable and the seasonality in NDVI (the difference between minimum and maximum NDVI) as an explanatory variable (RES1, **a**); (ii) residuals from OLS regressions between seasonality in NDVI as a response variable and maximum NDVI as an explanatory variable (RES2, **b**), (iii) maximum NDVI and NDVI seasonality within selected subsets of the whole dataset (see Methods, Figs 2 and S8). The figure shows relationships between assemblage mean clutch size and maximum NDVI for the dataset with restricted variation in NDVI seasonality (**c**), and relationships between assemblage mean clutch size and seasonality in NDVI for the dataset with restricted variation in maximum NDVI (**d**). Grey areas indicate confidence intervals.



Chapter 3

Received: 19 November 2018 | Revised: 16 July 2019 | Accepted: 22 July 2019

DOI: 10.1111/geb.12997

RESEARCH PAPER

Global Ecology and Biogeography A Journal of Macroecology WILEY

Global diversity patterns are modulated by temporal fluctuations in primary productivity

Anna Toszogyova[1,2] | **David Storch**[1,2]

[1]Center for Theoretical Study, Charles University and the Academy of Sciences of the Czech Republic, Prague, Czech Republic

[2]Department of Ecology, Faculty of Science, Charles University, Prague, Czech Republic

Correspondence
Anna Toszogyova, Center for Theoretical Study, Charles University and the Academy of Sciences of the Czech Republic, Jilská 1, 110 00 Prague, Czech Republic.
Email: anna83@seznam.cz

Funding information
Grantová Agentura České Republiky, Grant/Award Number: 16-26369S

Editor: Véronique Boucher-Lalonde

Abstract

Aim: To evaluate the role of seasonal and non-seasonal productivity fluctuations in global patterns of species richness.

Location: Worldwide.

Time period: 2000–2017.

Major taxa studied : Amphibians, birds, mammals.

Methods: We analysed time series of monthly variation of the Normalized Difference Vegetation Index (NDVI), a surrogate of primary productivity, within *c*. 100 km × 100 km cells across all continents, estimating the mean, periodic seasonal variation and aperiodic unpredictable fluctuations of the NDVI in these cells. We then explored the relationships between mean NDVI and the components of its temporal variation and evaluated the independent effects of the above-mentioned variables on species richness in the three vertebrate groups by means of variation partitioning.

Results: There is a hump-shaped relationship between mean productivity and variation in productivity, so that temporal variation in productivity is lowest in regions with minimum and maximum values of mean productivity. Although mean productivity is a strong determinant of species richness, both seasonal and non-seasonal productivity variation significantly affect the species richness of all studied taxa when accounting for mean productivity. However, the direction of these effects differs between regions differing in the mean productivity level. High variation in productivity has a negative effect on species richness in regions with moderate to high productivity levels, whereas species richness is higher in arid regions with high variation in productivity.

Main conclusions: Species richness is affected by temporal variation in productivity, but these effects differ regionally. In productive areas, high environmental stochasticity may increase population extinction rates, whereas arid regions probably benefit from resource fluctuations that promote species coexistence. Our results indicate that contemporary changes in patterns of temporal resource fluctuations may affect future global patterns of biological diversity on Earth.

KEYWORDS
diversity–productivity relationship, environmental unpredictability, latitudinal diversity gradient, productivity fluctuations, species richness patterns, storage effect

1 | INTRODUCTION

Species richness patterns are ultimately driven by the processes of speciation, colonization and extinction. These processes are modulated by the environment, leading to relatively predictable spatial diversity patterns (Hawkins et al., 2012). The most pronounced large-scale diversity pattern is the positive correlation between the number of species and climatic variables related to energy availability, namely precipitation, temperature and environmental productivity (e.g., Currie, 1991; Field et al., 2009; Hawkins, Field, et al., 2003; Jetz & Fine, 2012). Although there are several hypotheses explaining this climate–richness or species–energy relationship (Currie et al., 2004; Storch, 2012), three major mechanisms are especially important: High temperature can promote higher speciation rates (Allen, Gillooly, & Brown, 2007; Allen, Gillooly, Savage, & Brown, 2006); long-term climatic stability may lead to lower extinction rates and/or more time to adaptation, resulting in a higher number of coexisting species (Jablonski, Roy, & Valentine, 2006; Kozak & Wiens, 2012; Ricklefs, 2006; Wiens & Donoghue, 2004); and high environmental productivity may allow the persistence of higher total number of individuals and, consequently, a higher number of species with viable populations (Brown, 1981; Evans, Warren, & Gaston, 2005; Gaston, 2000; Srivastava & Lawton, 1998; Storch, Bohdalková, & Okie, 2018; Wright, 1983; Wright, Currie, & Maurer, 1993).

Recently, evidence has accumulated that high speciation rates are not systematically higher in areas with high species richness (Rabosky, Title, & Huang, 2015; Rabosky et al., 2018; Schluter, 2016) and although hot and humid tropical areas often host ancient lineages, species richness patterns seem to be largely decoupled from diversification history; although some regions are species-rich as a result of a long time for species accumulation, other regions have been colonized in relatively recent times and have reached high diversity due to high diversification rates (Belmaker & Jetz, 2015; Oliveira et al., 2016). This can be interpreted so that each region has a particular limit for species richness and this “carrying capacity for species richness” (Storch & Okie, 2019) can be reached either by slow species accumulation or by rapid diversification (Rabosky & Hurlbert, 2015). These limits probably emerge via the effect of environmental productivity on the number of viable populations that can persist in given environment (Gaston, 2000): For given amount of resources (or energy inflow), an increase of the number of species beyond particular levels necessarily leads to decreasing population sizes and, consequently, increasing extinction rates above the rate of species origination (Storch et al., 2018). Macroecological diversity patterns thus seem to be largely driven by population size-dependent extinction dynamics modulated by resource abundance (Rabosky & Hurlbert, 2015; Storch et al., 2018).

This has important implications. If the extinction dynamic is crucial for producing large-scale diversity patterns, it is reasonable to expect that all the factors that affect extinction rates beyond the effects of population sizes should also affect large-scale diversity patterns. Therefore, species richness is expected to be lower in environments characterized by greater short-term resource fluctuations, because these increase population fluctuations and thus extinction rates beyond the sole effect of population size (Ovaskainen & Meerson, 2010). Intuitively, any environment exhibiting higher environmental stochasticity and, consequently, higher extinction probability should, everything else being equal, host a lower number of species than an environment that is more stable or predictable. Environmental productivity is therefore predicted to affect species richness both by affecting the potential number of species with viable populations (Gaston, 2000) and via its temporal variation, by affecting the viability of populations through the extent of their fluctuations (Adler & Drake, 2008; Boyce, 1992; Lande, 1993).

Some studies have addressed the role of environmental fluctuations and their predictability on patterns of species distribution and diversity (Chesson & Huntly, 1997; Letten, Ashcroft, Keith, Gollan, & Ramp, 2013; Tonkin, Bogan, Bonada, Rios-Touma, & Lytle, 2017). However, most of these studies focused on running-water ecosystems and considered local scales only (Tonkin et al., 2017), or they did not test the effect of environmental fluctuations on species richness patterns (Jiang, Felzer, Nielsen, & Medlyn, 2017; Poff & Ward, 1989; Steel & Lange, 2007). Moreover, most studies on the role of environmental variation in determining species richness have explored only the effect of seasonality (Dalby, McGill, Fox, & Svenning, 2014; Gouveia, Hortal, Cassemiro, Rangel, & Diniz-Filho, 2013; Hurlbert & Haskell, 2003) and not the unpredictable component of environmental variation (but see Letten et al., 2013). In this respect, some studies have explored variation in temperature and precipitation (Jiang et al., 2017; Letten et al., 2013; Tonkin et al., 2017). However, although the observed patterns are illuminating (see Jiang et al., 2017), and temperature and precipitation surely affect species distribution and richness, these variables represent only the ultimate drivers of diversity patterns, acting through their effects on biological rates (Brown, Gillooly, Allen, Savage, & West, 2004) or resource levels (Storch, 2012). For this reason, we focus on a more proximate driver of species richness, namely environmental productivity (understood as the amount of available resources for all terrestrial animal groups), whose mean level as well as year-to-year fluctuations are predicted to drive extinction rates and, consequently, species richness.

Here, we test this prediction using data on global species richness patterns in three major vertebrate classes for which we have good global distributional data (amphibians, birds and mammals) and long-term data on resource fluctuations across the terrestrial surface of the Earth. We assume that resource availability for these vertebrate groups can be estimated based on a surrogate of net primary productivity, namely the Normalized Difference Vegetation Index (NDVI), which represents an estimate of the vegetation cover and its temporal changes. Thanks to the relatively long time series of NDVI, it is possible to analyse temporal variation in this surrogate of primary productivity and to decompose it into its periodic (seasonal) aspect and aperiodic component, which is essentially unpredictable. This is crucial because the periodic component of resource variation can have potentially very different consequences for species population dynamics compared with unpredictable environmental variation. Most importantly, although seasonality may act as an environmental filter (Gouveia, Hortal, Cassemiro, Rangel, & Diniz-Filho, 2013), species are able to adapt to seasonal oscillations by adjusting their life cycles; for example, by breeding during the favourable productive season or through dormancy, hibernation, energy storage or seasonal migrations during the harsh, unproductive season (Varpe, 2017; Williams et al., 2017). Consequently, periodic seasonal resource variation may not promote population fluctuations, although it may still affect the probability of population extinction by affecting overall population abundance; long-term mean population size is often determined by minimum resource availability over the course of the year (Hořák, Tószögyová, & Storch, 2015).

In contrast, aperiodic unpredictable resource fluctuations very probably have a direct effect on population dynamics and increase the chance that such dynamics will eventually lead to extinctions (Adler & Drake, 2008; Boyce, 1992; Ovaskainen & Meerson, 2010). Besides this effect, unpredictable environments impose additional filters on species occurrence (Tonkin et al., 2017), selecting for generalism and fast life strategies, which may impede coexistence. On the other hand, environmental fluctuation may, in some situations, promote species coexistence, e.g., via the storage effect (Chesson, 2000b). This occurs if abundant species compete fiercely during periods of resource peaks, whereas rare species can survive periods of resource scarcity by storing resources amassed during more favourable periods. The effect of resource fluctuation thus may not be only detrimental in terms of resulting species richness. Our aim was to test the effects of both periodic (seasonal) and aperiodic resource fluctuations on global species richness patterns of three classes of vertebrates to evaluate and compare the roles of mean productivity and its temporal fluctuations in macroecological diversity patterns.

2 | METHODS

Our time series of environmental productivity were composed of values of the MODIS-derived NDVI obtained from the NASA Land Processes Distributed Active Archive Center (LP DAAC) (https://lpdaac.usgs.gov/products/mod13c2v006/). The NDVI quantifies remotely sensed vegetation greenness, which is an appropriate proxy for the amount of available resources for all terrestrial animal groups (Gordo, 2007; Lafage, Secondi, Georges, Bouzillé, & Pétillon, 2014; Lassau & Hochuli, 2008). We could have used some other measures of environmental productivity, including the MODIS-based Net Primary Productivity, but such data typically do not provide sufficiently long and well-resolved time series. Moreover, because they are a result of complex models with many hidden assumptions, there is no evidence that they reflect real ecosystem productivity better than remotely sensed data obtained by more direct means (Šímová & Storch, 2017).

The global NDVI dataset consists of time series of 205 monthly averages over the period between February 2000 and February 2017, with a spatial resolution of 0.05°. We converted these data into a 1° equal-area map to make them compatible with species distributional data. We are aware of the fact that the 17 years-long time series is too short and too recent to represent the environmental variation that affected species richness patterns in our data, namely given that the species distribution data that we used integrate knowledge on species distributions collected over a much longer period. However, we assume that our relatively recent time series is representative in terms of capturing general properties of environmental variation in different places, at least during the last few centuries. It is probable that the overall global pattern of temporal environmental variation is relatively stable, so that the areas which reveal high seasonality and/or unpredictability during a recent 17 years-long time window were characterized by these properties also in previous decades or centuries, although it is possible that temporal variation

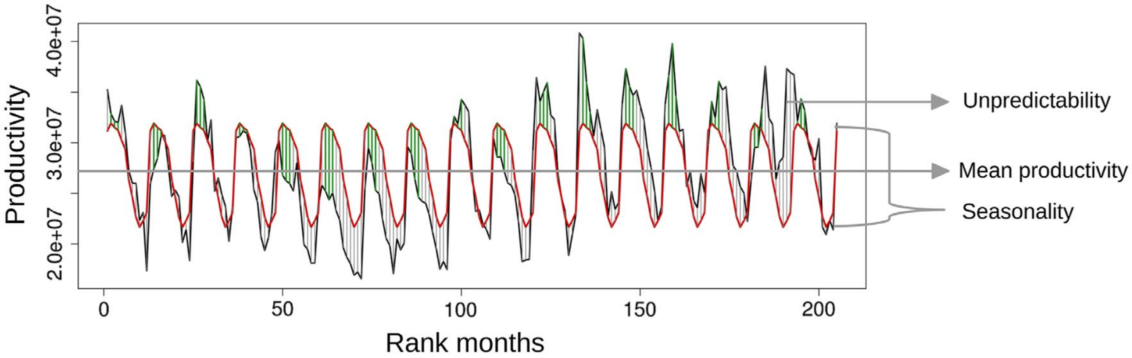


FIGURE 1 Time series of monthly values of environmental productivity [Normalized Difference Vegetation Index (NDVI)] over a period of 205 months (17 years) for one grid cell (black line). The red line represents the periodic seasonal trend constructed using mean values of the NDVI for each month over the 17 year period. Mean productivity is calculated as the mean value of the seasonal cycle. Seasonality is represented by the range of the seasonal cycle (i.e., the difference between the average minimum and average maximum productivity level). The vertical grey lines represent the residuals from the seasonal cycle. Unpredictability was calculated as the standard deviation of the residuals from the seasonal trend. The vertical green lines represent unpredictability in the productive season (i.e., the standard deviation of residuals from the three on average most productive months)

in productivity was slightly more or less pronounced in particular regions during the more distant past.

The data on the distributions of mammalian and amphibian species were provided by the IUCN Global Species Programme (http://www.iucnredlist.org), and data on the distributions of avian species were obtained from BirdLife International (http://www.birdlife.org). These two databases contained distributional information on species ranges in geo-referenced polygons on 5,298 terrestrial mammal, 10,961 bird and 6,493 amphibian species (extinct species were excluded, and the species were included regardless of their seasonal presence), which we transformed into a 1° (~100.2 km) spatial grid using the Mollweide coordinate system (equal-area projection). The datasets of NDVI and all three taxa consisted of 12,606, 12,608 and 11,315 grid cells for mammals, birds and amphibians, respectively.

We decomposed the NDVI time series for each grid cell into three components: (a) mean; (b) seasonality; and (c) non-periodic fluctuations (unpredictability). First, we filtered out the overall linear or quadratic trend (depending on which one better captured the overall temporal pattern) over the whole 17 year period. The seasonal cycle was then constructed using the mean value of the NDVI for each month across the entire 17 year period, and this oscillation (17 times over the whole time period) was taken as the basis for calculating unpredictability using the residuals from this curve. Three variables were then calculated for each grid cell. *Mean productivity* was the mean NDVI value of the seasonal cycle (the same value as the mean NDVI value across all years) (Figure 1). *Seasonality* was the difference between the average maximum and average minimum productivity level (the range of the seasonal cycle) (Figure 1). *Unpredictability* was quantified based on the standard deviation of residuals from the periodic seasonal trend (Figure 1). Originally, we calculated several variables characterizing random non-periodic fluctuations using these residuals (Supporting Information Appendix S1), later selecting the best variable that explained most of the variance in species richness. It turned out that, besides unpredictability as defined above, unpredictability in the productive season (residuals from the three on average most productive months) was, in some cases, an especially strong predictor of species richness. We thus also explored the effect of this additional variable on species richness. For the purposes of the analyses, it was appropriate to use logarithmic transformation (base 10) of seasonality and unpredictability and of the species richness of birds and amphibians and square-root transformation of species richness of mammals, to ensure an approximately normal distribution of residuals of respective models. Mean productivity was not transformed.

We used a variation partitioning analysis to distinguish the separate independent explanatory effects of the three aforesaid variables on species richness. The variation partitioning was based on partial linear regression models. Following Peres-Neto, Legendre, Dray, and Borcard (2006), we applied the function of the variation partitioning analysis that provides adjusted R^2 to assess the variance explained by the explanatory variables and their combinations, because it is the only unbiased method. To estimate the significance of individual effects, we constructed generalized least squares regression models, with a spatial correlation structure to control for spatial autocorrelation. All analyses were performed in the R statistical computing environment (R Development Core Team, 2017).

3 | RESULTS

The species richness of all three groups was positively related to mean productivity (Figure 2a; Supporting Information Figure S1a). In contrast, the relationship between species richness and both seasonality and unpredictability was universally triangular, so that low seasonality and unpredictability allowed for both low and high richness values, whereas high values of these variables were uniformly associated with low richness (Figure 2b,c; Supporting Information Figure S1b,c). This pattern, however, was strongly affected by covariance between both the variables and mean NDVI; both seasonality and unpredictability reached their highest values in the temperate zone of the Northern Hemisphere and in less productive regions

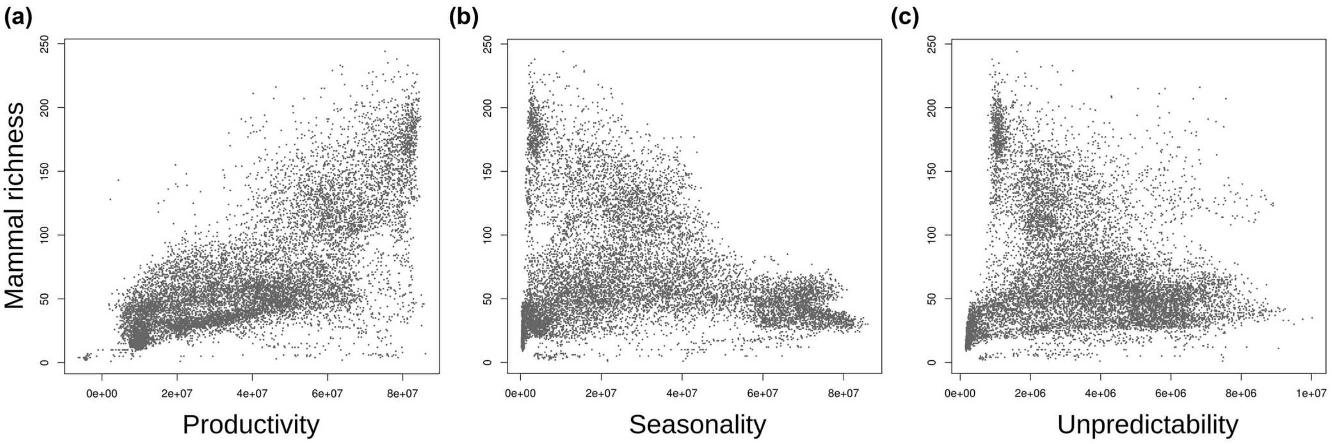


FIGURE 2 Relationships between the species richness of mammals and mean productivity (a), seasonality (b) and unpredictability (c). All these relationships are very similar in birds and amphibians (see Supporting Information Figure S1)

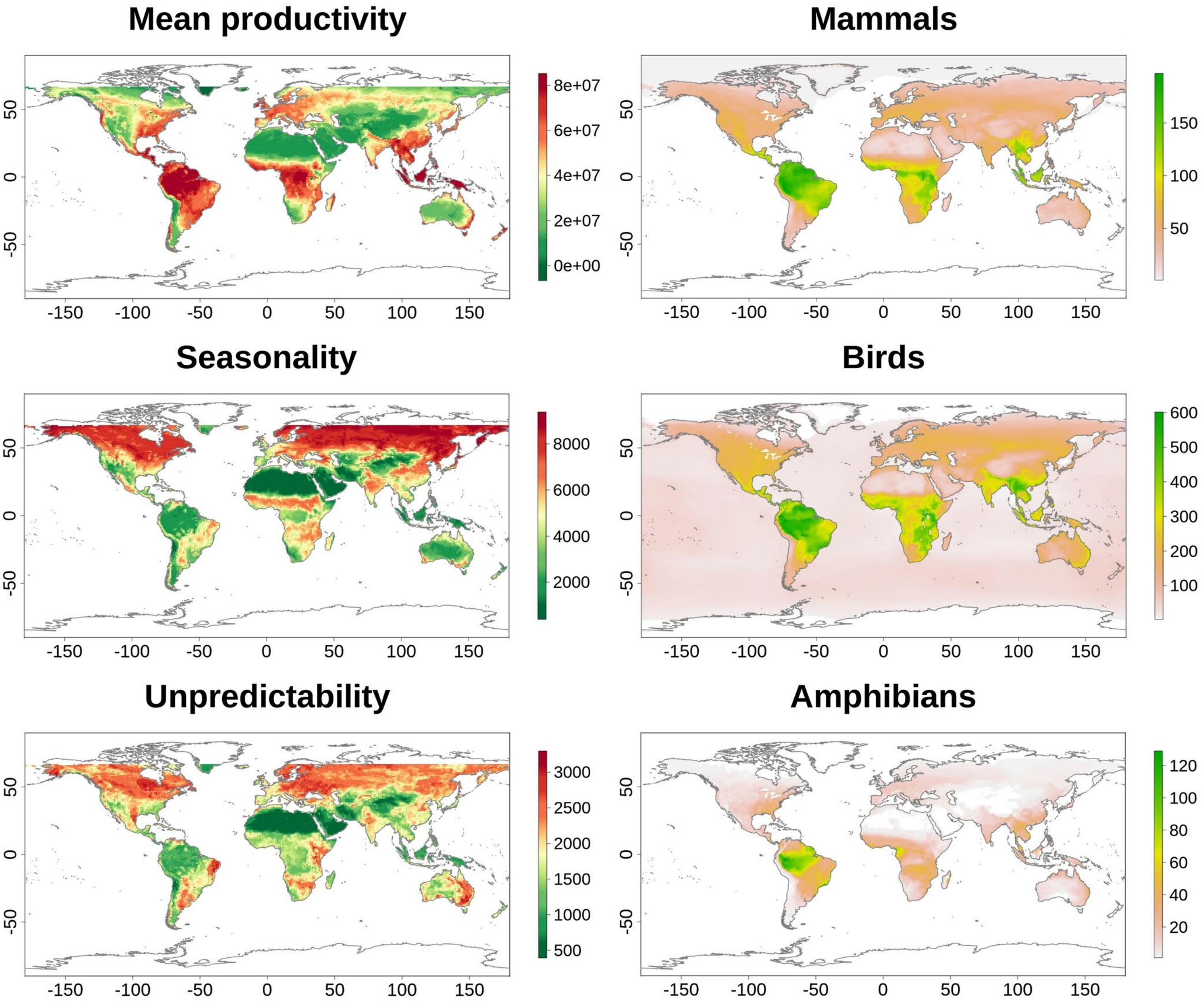


FIGURE 3 Left panels show geographical patterns of mean productivity, seasonality (square-root transformed) and unpredictability (square-root transformed). The highest values (red) of mean productivity occur in the tropics, whereas the highest values of seasonality and unpredictability are found in temperate regions. The lowest (green) variations in productivity, both seasonal and unpredictable, are distributed both in the wet tropics and in arid areas. Right panels show patterns of global species richness of the three taxonomic groups under study

of the tropics of the Southern Hemisphere (Figure 3). In contrast, low values of both these variables (seasonality and unpredictability) characterizing temporal variation in productivity occurred not only in the productive tropics, but also in deserts. The overall relationship between mean productivity and temporal variation in productivity is therefore hump shaped (Figure 4), which implies that the effect of mean productivity on species richness could not be simply controlled for by using the residuals from the linear regression of productivity variation on mean productivity.

Although quadratic regression fitted on the hump-shaped relationship between mean productivity and variation in productivity could potentially have solved this problem, its fit was rather poor, and using residuals from this function would lump together regions with similar relative productivity fluctuations but extremely different mean productivity. For these reasons, we decided to explore the effects of productivity-controlled seasonality and unpredictability on species richness by dividing the dataset into three contrasting segments (regions) differing in their bivariate relationships between mean productivity and variation in productivity. Within each of these regions, the relationship between mean productivity and variation in productivity was linear (Figure 4), which enabled the testing of the independent effects by variation partitioning. These three segments roughly correspond to arid regions, temperate regions and the wet tropics, and the effects of mean productivity-controlled seasonality and unpredictability were tested separately for each region. Given that the division of the globe based on the

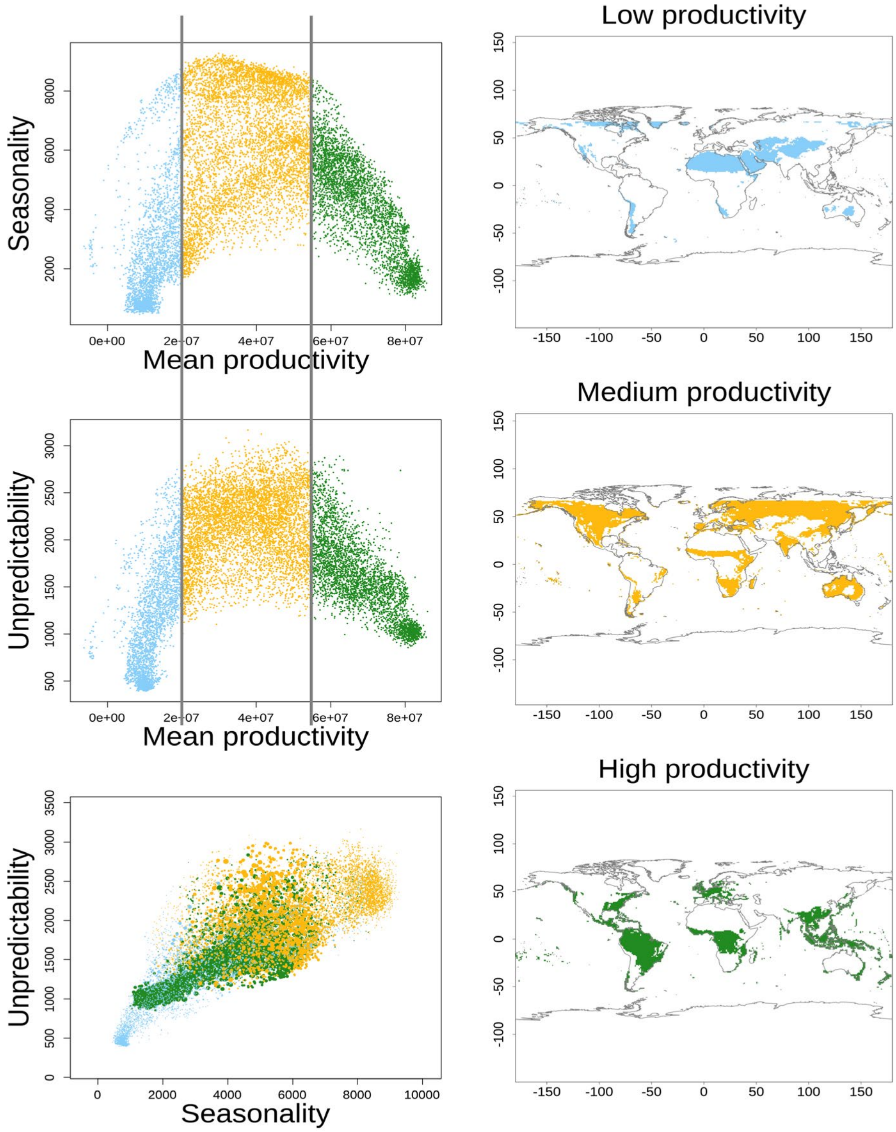


FIGURE 4 Left panels show relationships between mean productivity and seasonality (top) and unpredictability (middle), respectively. Based on these hump-shaped relationships, we distinguished three groups of regions: Regions with low productivity and a positive mean–variation relationship (blue); regions with medium productivity and no mean–variation relationship (yellow); and regions with high productivity and a negative mean–variation relationship (green). The bottom panel shows the correlation between seasonality and unpredictability; the size of the dots corresponds to the species richness of mammals, as an example. Right panels show maps of the corresponding three regions. With the exception of mean productivity, all the variables were square-root transformed

hump-shaped relationship is partly arbitrary, we checked the results for robustness by shifting the dividing lines in both directions, confirming that alternative divisions did not affect the results (Supporting Information Figure S2).

Variation partitioning revealed that all the three components of our productivity time series independently affected the species richness of all three groups of vertebrates, albeit differently in the three different regions (Figures 5 and 6; Supporting Information Table S1). In low-productivity (arid) regions, the sole effect of unpredictability had the strongest positive effect on species richness in birds and mammals, whereas in amphibians the effect of seasonality was slightly greater, although this was not significant after accounting for spatial autocorrelation (see below). In low-productivity areas, all the effects of mean productivity, seasonality and unpredictability were positive. Unpredictability in the productive season was an even stronger predictor of species richness in arid regions, explaining (independently of mean productivity and seasonality) 15%, 23% and 13% of species richness variation in mammals, birds and amphibians, respectively (Figures 5b and 6b; Supporting Information Table S1). In regions with medium productivity (temperate), which

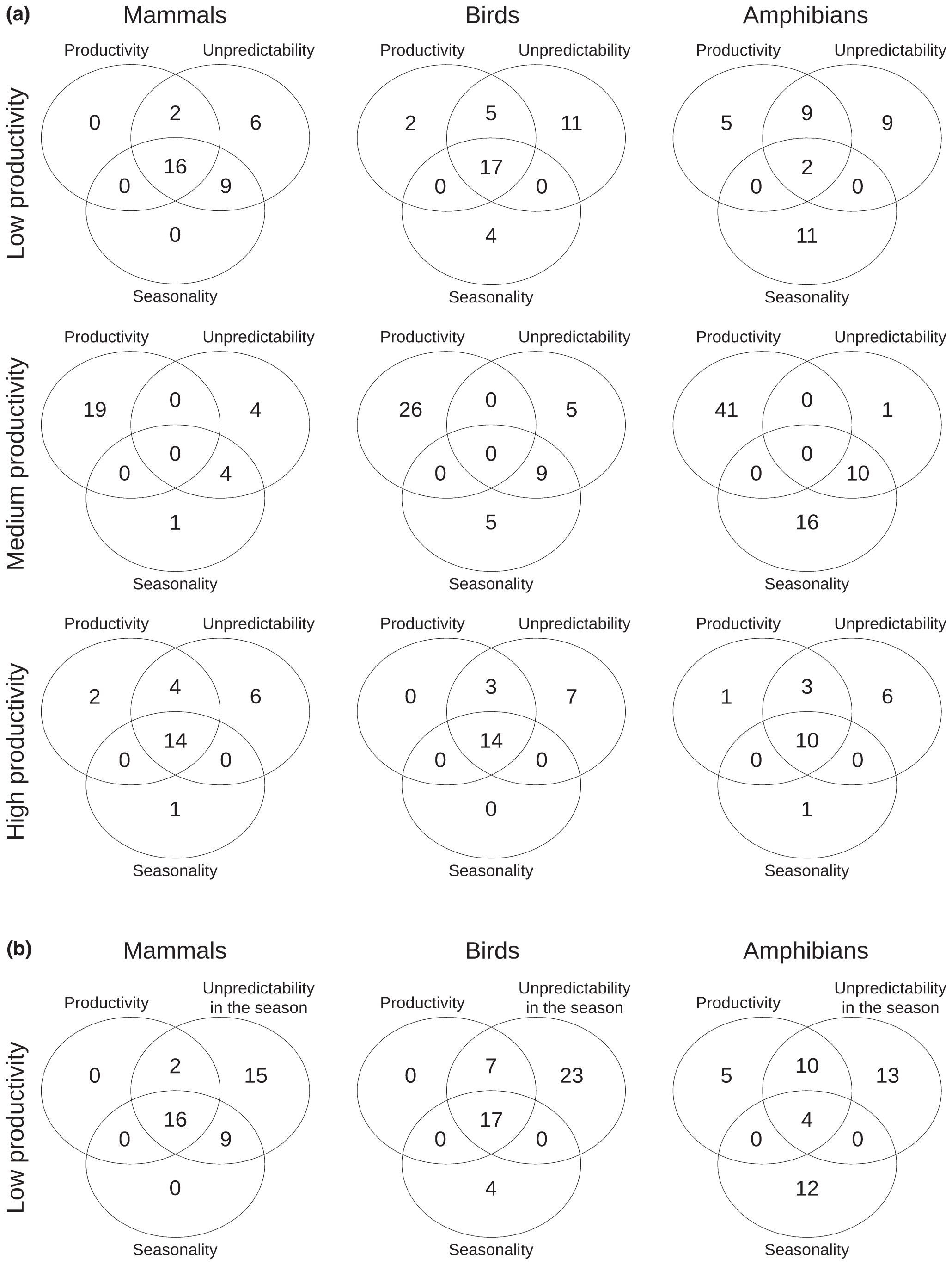


FIGURE 5 (a) Venn diagrams describing variation partitioning for the species richness of mammals, birds and amphibians by mean productivity and productivity seasonality and unpredictability in the three distinct regions (see Figure 4). (b) Variation partitioning for the species richness of mammals, birds and amphibians by mean productivity and its seasonality and unpredictability in the productive season in low-productivity regions. The diagrams show adjusted R^2 values (rounded) associated with each partition or for overlapping partitions. The separate independent effects of all explanatory variables were significant (after accounting for spatial autocorrelation) in their contributions to species richness (see Supporting Information Table S2). Unpredictability, especially during the productive season, was the strongest predictor of species richness in arid areas

exhibited no relationship between mean productivity and variation in productivity, unpredictability and seasonality did not show a strong effect on species richness (except in amphibians, where the effect of seasonality was strong and negative), whereas mean productivity affected species richness positively. Similar effects were observed in highly productive regions (wet tropics), in which unpredictability turned out to have a negative effect on species richness, whereas the sole independent effect of seasonality was

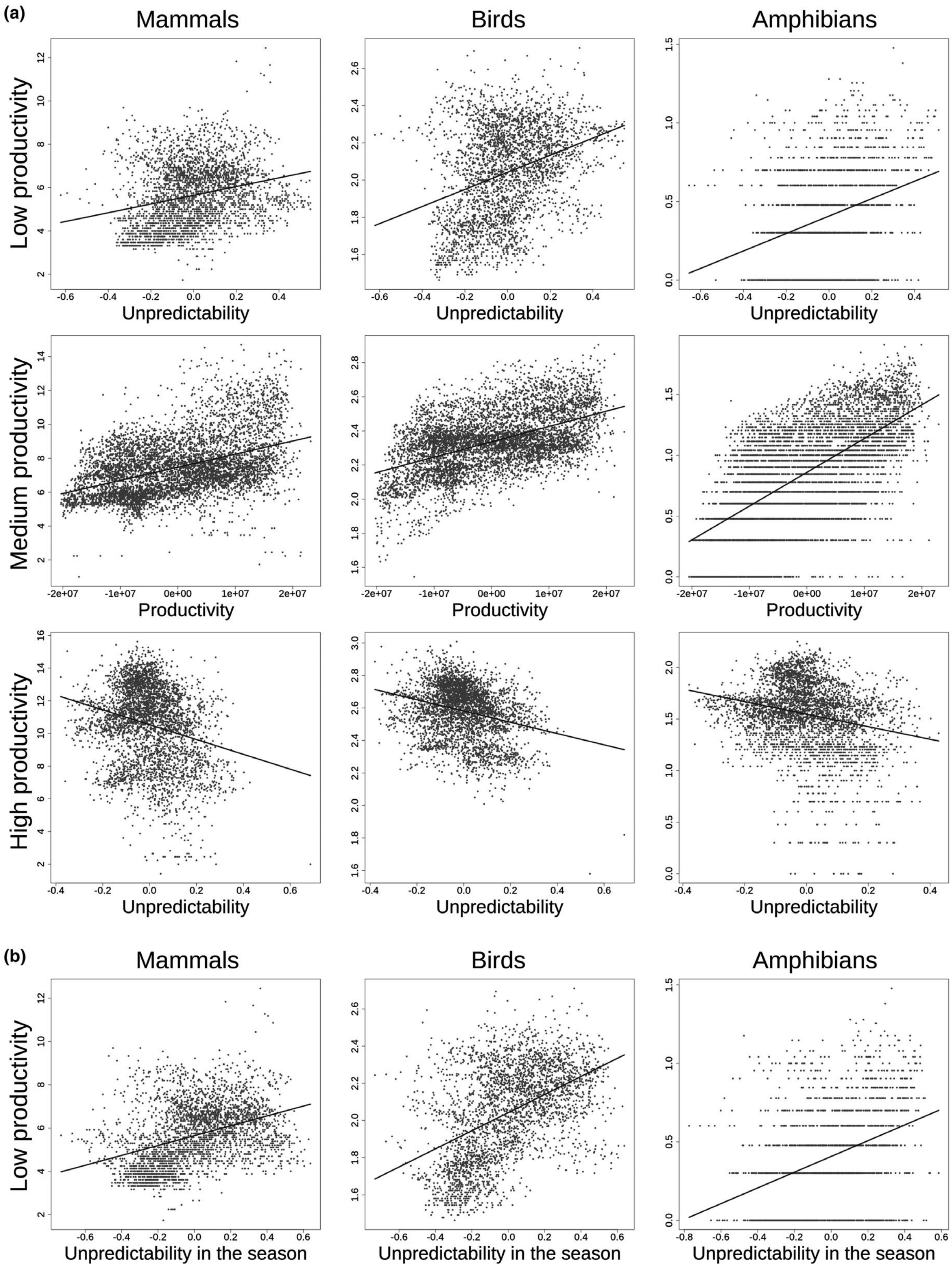


FIGURE 6 (a) Relationships between the species richness of mammals, birds and amphibians, and the sole effect (controlling for all the other effects) of the strongest environmental predictors (out of mean productivity, seasonality and unpredictability for the given vertebrate classes and regions). In the case of amphibians in the low-productivity region, we used the second strongest predictor, because the strongest predictor (seasonality) was not significant after accounting for spatial autocorrelation (see Supporting Information Table S2). (b) Relationship between species richness and mean productivity- and seasonality-controlled unpredictability during the productive season in the region with the lowest productivity. With the exception of mean productivity, all the variables were $\log_{10}$-transformed, and mammalian species richness was square-root transformed

very weak or non-existent. Similarly as in arid areas, unpredictability had the strongest independent effect on species richness, but in the opposite direction: Productive but relatively unpredictable areas had lower species richness than areas with stable and predictable productivity. In these two types of regions (moderately and highly productive ones), unpredictability in the productive season had an equal or slightly weaker effect than total unpredictability measured over the course of the whole year (not shown). Spatial generalized least squares models revealed that the relationship between species richness and all environmental variables (after accounting for the effects of the other variables) was statistically significant even after removing spatial autocorrelation, with the exception of the effect of seasonality on amphibian species richness in the arid areas (Supporting Information Table S2).

4 | DISCUSSION

Temporal resource variation should, in theory, affect species richness (e.g., Storch et al., 2018). However, the testing of this idea at a macroecological scale has been impeded by the lack of appropriate data and the complex covariation of the measures of environmental variation with other environmental predictors, namely mean productivity (which is known to be a good determinant of vertebrate species richness globally; Belmaker & Jetz, 2011; Davies et al., 2007; Hawkins, Field, et al., 2003; Hawkins, Porter, & Diniz-Filho, 2003; Wright et al., 1993). We found a nonlinear (hump-shaped) covariation between mean productivity and temporal productivity variation, expressed as seasonality and unpredictability (representing residuals from regular seasonal variation), respectively. Such non-linearity is expected, as regions with both the highest and the lowest productivity must necessarily exhibit relatively low productivity variation (otherwise, they could not reach extreme values of mean productivity). Such a relationship between mean productivity and its variation, however, implies the existence of three distinct types of environment differing in the regime of covariation between mean productivity and its variation. Arid areas are characterized by positive covariation of mean productivity and its temporal variation, whereas temperate areas with intermediate productivity are characterized by the absence of a relationship between these variables, and wet tropical areas reveal a negative relationship between mean productivity and its temporal variation, with the most productive areas simultaneously being very stable. Because of these basic differences, we treated the three types of environments or regions independently. We suggest that future analyses of the role of variation in productivity should account for these substantial differences between the major types of environment. The complex relationship between the mean value of productivity and its variation probably lies behind the scarcity of studies addressing these effects across large geographical extents.

In most productive areas, and partly also in areas with moderate productivity, the number of species decreases with both the seasonality and the unpredictability of productivity, when accounting for the overwhelming effect of mean productivity. This is in accord with the general notion that temporal resource fluctuations lead to more dramatic population dynamics, increasing extinction rates (Lande, 1993; Ovaskainen & Meerson, 2010), and with the formalization of this notion in the theory of Storch et al. (2018). The effects of seasonality and unpredictability are difficult to distinguish because of their covariation, but it is probable that both these effects may increase the probability that a local population will go extinct, albeit via a slightly different mechanism. Seasonality may decrease effective population size (Hořák et al., 2015), whereas unpredictability probably increases the extent of stochastic population fluctuations, which increase the chance that a population of given size goes extinct (Adler & Drake, 2008; Boyce, 1992; Lande, 1993).

The most surprising result is the positive effect of productivity unpredictability on species richness in unproductive areas. Although unpredictability can affect population fluctuations and thus increase the probability of stochastic extinction, it is possible that arid areas with unpredictable resource pulses are, for many species, more favourable than arid regions with stable (i.e., constantly low) resource levels. Unpredictable resource fluctuations may also increase the chances of species coexistence via the storage effect (Adler & Drake, 2008; Cáceres, 1997; Chesson, 2000a, 2000b; Chesson & Warner, 1981). Species may benefit from resource surplus in favourable periods and survive in adverse periods by storing energy resources, migrating (many desert birds are very mobile) or entering diapause (many desert frogs). At the same time, no species competitively prevails in such an environment, because high population growth in favourable periods leads to overcrowding of competitively superior species (Chesson, 2000b). In addition, some resources, such as seeds, are produced by plants during peaks of vegetation production, but they may persist as a food source also in subsequent periods. All these effects are in line with our observation that unpredictability in the productive season, corresponding mostly to an unpredictable excess of resources, was the best predictor of species richness in arid regions. In contrast, arid areas with constantly low production may host species with relatively stable (albeit small) population sizes, which utilize the majority of available production, thus limiting access to resources for other species.

Assuming that the relatively short time window during which we analysed temporal variation in NDVI provides a proper representation of the large-scale patterns of temporal productivity fluctuations, it appears that both predictable (seasonal) and unpredictable temporal variation in productivity affect species richness patterns. This can have serious implications for our ability to predict future changes in biodiversity linked to global climate change. Both increases and decreases in both the periodic and aperiodic components of variation in productivity can be expected in the future, and they will probably lead to further redistribution of biological diversity (Bonada, Dolédec, & Statzner, 2007; Tonkin et al., 2017). There is no doubt that mean values of climatic variables, including temperature and primary productivity, are important; changes in mean values have already been shown to be altering the current biota. However, temporal variation of these variables may turn out to be even more important and, probably, less predictable (Letten et al., 2013).

In sum, our results show that temporal variation in primary productivity affects global patterns of vertebrate species richness. Although mean productivity is a strong determinant of species richness, probably through its effect on the number of viable populations that can persist in a given environment (Gaston, 2000; Storch et al., 2018; Wright et al., 1993), productivity fluctuations can affect the viability of populations through its effect on the extent of population fluctuations (Lande, 1993; Ovaskainen & Meerson, 2010). Although the effect of regular annual oscillations of productivity (seasonality) may differ from that of productivity unpredictability, these two components of the variation in productivity are so highly correlated that they cannot be distinguished easily. Nevertheless, productivity unpredictability seems slightly more important in its effect on species richness patterns. In line with our original expectation, variation in productivity decreases species richness in areas with moderate to high productivity. However, in contrast to our expectation, its effect is the opposite in arid areas, where elevated variation in productivity leads to higher species richness, probably because resource fluctuations have a positive influence on species coexistence in such resource-poor environments. These findings imply that future diversity patterns may be strongly affected not only by gradual changes of the means of various environmental variables, such as temperature and precipitation, but also by changing regimes of environmental fluctuations and temporal variation of resource levels.

ACKNOWLEDGMENTS

This research was supported by the Czech Science Foundation (grant no. 16-26369S). We are grateful to Pedro Peres-Neto for inspiring discussions on this topic, and to Antonín Macháč for the comments on an earlier draft of the manuscript.

DATA AVAILABILITY

The data that support the findings of this study are openly available at http://www.iucnredlist.org/, version no. 2017-1, downloaded on 23 May 2017, and available on request at http://datazone.birdlife.org/species/requestdis/, version 6.0 and at https://e4ftl01.cr.usgs.gov/MODV6_Cmp_C/MOLT/MOD13C2.006/, version MOD13C2 V006, https://doi.org/10.5067/MODIS/MOD13C2.006.

ORCID

Anna Toszogyova https://orcid.org/0000-0001-6084-625X

David Storch https://orcid.org/0000-0001-5967-1544

REFERENCES

Adler, P. B., & Drake, J. M. (2008). Environmental variation, stochastic extinction, and competitive coexistence. *The American Naturalist*, *172*, 186–195. https://doi.org/10.1086/591678

Allen, A. P., Gillooly, J. F., & Brown, J. H. (2007). Recasting the species–energy hypothesis: The different roles of kinetic and potential energy in regulating biodiversity. In D. Storch, P. Marquet, & J. H. Brown (Eds.), *Scaling biodiversity (ecological reviews)* (pp. 283–299). Cambridge: Cambridge University Press.

Allen, A. P., Gillooly, J. F., Savage, V. M., & Brown, J. H. (2006). Kinetic effects of temperature on rates of genetic divergence and speciation. *Proceedings of the National Academy of Sciences USA*, *103*, 9130–9135. https://doi.org/10.1073/pnas.0603587103

Belmaker, J., & Jetz, W. (2011). Cross-scale variation in species richness–environment associations. *Global Ecology and Biogeography*, *20*, 464–474. https://doi.org/10.1111/j.1466-8238.2010.00615.x

Belmaker, J., & Jetz, W. (2015). Relative roles of ecological and energetic constraints, diversification rates and region history on global species richness gradients. *Ecology Letters*, *18*, 563–571. https://doi.org/10.1111/ele.12438

BirdLife International and Handbook of the Birds of the World (2017). Bird species distribution maps of the world. Version 6.0. Retrieved from http://datazone.birdlife.org

Bonada, N., Dolédec, S., & Statzner, B. (2007). Taxonomic and biological trait differences of stream macroinvertebrate communities between mediterranean and temperate regions: Implications for future climatic scenarios. *Global Change Biology*, *13*, 1658–1671. https://doi.org/10.1111/j.1365-2486.2007.01375.x

Boyce, M. S. (1992). Population viability analysis. *Annual Review of Ecology and Systematics*, *23*, 481–506. https://doi.org/10.1146/annurev.es.23.110192.002405

Brown, J. H. (1981). Two decades of homage to Santa Rosalia: Toward a general theory of diversity. *American Zoologist*, *21*, 877–888. https://doi.org/10.1093/icb/21.4.877

Brown, J. H., Gillooly, J. F., Allen, A. P., Savage, V. M., & West, G. B. (2004). Toward a metabolic theory of ecology. *Ecology*, *85*, 1771–1789. https://doi.org/10.1890/03-9000

Cáceres, C. E. (1997). Temporal variation, dormancy, and coexistence: A field test of the storage effect. *Proceedings of the National Academy of Sciences USA*, *94*, 9171–9175. https://doi.org/10.1073/pnas.94.17.9171

Chesson, P. L. (2000a). Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics*, *31*, 343–366. https://doi.org/10.1146/annurev.ecolsys.31.1.343

Chesson, P. L. (2000b). General theory of competitive coexistence in spatially-varying environments. *Theoretical Population Biology*, *58*, 211–237. https://doi.org/10.1006/tpbi.2000.1486

Chesson, P. L., & Huntly, N. (1997). The roles of harsh and fluctuating conditions in the dynamics of ecological communities. *The American Naturalist*, *150*, 519–553. https://doi.org/10.1086/286080

Chesson, P. L., & Warner, R. R. (1981). Environmental variability promotes coexistence in lottery competitive systems. *The American Naturalist*, *117*, 923–943. https://doi.org/10.1086/283778

Currie, D. J. (1991). Energy and large-scale patterns of animal- and plant-species richness. *The American Naturalist*, *137*, 27–49. https://doi.org/10.1086/285144

Currie, D. J., Mittelbach, G. G., Cornell, H. V., Field, R., Guegan, J.-F., Hawkins, B. A., … Turner, J. R. G. (2004). Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, *7*, 1121–1134. https://doi.org/10.1111/j.1461-0248.2004.00671.x

Dalby, L., McGill, B. J., Fox, A. D., & Svenning, J.-C. (2014). Seasonality drives global-scale diversity patterns in waterfowl (Anseriformes) via temporal niche exploitation. *Global Ecology and Biogeography*, *23*, 550–562. https://doi.org/10.1111/geb.12154

Davies, R. G., Orme, C. D. L., Storch, D., Olson, V. A., Thomas, G. H., Ross, S. G., Gaston, K. J. (2007). Topography, energy and the global distribution of bird species richness. *Proceedings of the Royal Society B: Biological Sciences*, *274*, 1189–1197.

Didan, K. (2015). MOD13C2 MODIS/Terra Vegetation Indices Monthly L3 Global 0.05Deg CMG V006. *NASA EOSDIS Land Processes DAAC*. doi: https://doi.org/10.5067/MODIS/MOD13C2.006.

Evans, K. L., Warren, P. H., & Gaston, K. J. (2005). Species-energy relationships at the macroecological scale: A review of the mechanisms. *Biological Reviews of the Cambridge Philosophical Society*, *80*, 1–25. https://doi.org/10.1017/S1464793104006517

Field, R., Hawkins, B. A., Cornell, H. V., Currie, D. J., Diniz-Filho, J. A. F., Guégan, J.-F., … Turner, J. R. G. (2009). Spatial species-richness gradients across scales: A meta-analysis. *Journal of Biogeography*, *36*, 132–147. https://doi.org/10.1111/j.1365-2699.2008.01963.x

Gaston, K. J. (2000). Global patterns in biodiversity. *Nature*, *405*, 220–227.

Gordo, O. (2007). Why are bird migration dates shifting? A review of weather and climate effects on avian migratory phenology. *Climate Research*, *35*, 37–58. https://doi.org/10.3354/cr00713

Gouveia, S. F., Hortal, J., Cassemiro, F. A. S., Rangel, T. F., & Diniz-Filho, J. A. F. (2013). Nonstationary effects of productivity, seasonality, and historical climate changes on global amphibian diversity. *Ecography*, *36*, 104–113. https://doi.org/10.1111/j.1600-0587.2012.07553.x

Hawkins, B. A., Field, R., Cornell, H. V., Currie, D. J., Guégan, J.-F., Kaufman, D. M., … Turner, J. R. G. (2003). Energy, water, and broad-scale geographic patterns of species richness. *Ecology*, *84*, 3105–3117. https://doi.org/10.1890/03-8006

Hawkins, B. A., McCain, C. M., Davies, T. J., Buckley, L. B., Anacker, B. L., Cornell, H. V., … Stephens, P. R. (2012). Different evolutionary histories underlie congruent species richness gradients of birds and mammals. *Journal of Biogeography*, *39*, 825–841. https://doi.org/10.1111/j.1365-2699.2011.02655.x

Hawkins, B. A., Porter, E. E., & Diniz-Filho, J. A. F. (2003). Productivity and history as predictors of the latitudinal diversity gradient of terrestrial birds. *Ecology*, *84*, 1608–1623. https://doi.org/10.1890/0012-9658(2003)084[1608:PAHAPO]2.0.CO;2

Hořák, D., Tószögyová, A., & Storch, D. (2015). Relative food limitation drives geographical clutch size variation in South African passerines: A large-scale test of Ashmole's seasonality hypothesis. *Global Ecology and Biogeography*, *24*, 437–447. https://doi.org/10.1111/geb.12261

Hurlbert, A. H., & Haskell, J. P. (2003). The effect of energy and seasonality on avian species richness and community composition. *The American Naturalist*, *161*, 83–97. https://doi.org/10.1086/345459

IUCN. (2017). The IUCN red list of threatened species. Version 2017–1. Retrieved from http://www.iucnredlist.org

Jablonski, D., Roy, K., & Valentine, J. W. (2006). Out of the tropics: Evolutionary dynamics of the latitudinal diversity gradient. *Science*, *314*, 102–106.

Jetz, W., & Fine, P. V. A. (2012). Global gradients in vertebrate diversity predicted by historical area-productivity dynamics and contemporary environment. *PLoS Biology*, *10*, e1001292. https://doi.org/10.1371/journal.pbio.1001292

Jiang, M., Felzer, B. S., Nielsen, U. N., & Medlyn, B. E. (2017). Biome-specific climatic space defined by temperature and precipitation predictability. *Global Ecology and Biogeography*, *26*, 1270–1282. https://doi.org/10.1111/geb.12635

Kozak, K. H., & Wiens, J. J. (2012). Phylogeny, ecology, and the origins of climate–richness relationships. *Ecology*, *93*(sp8), S167–S181. https://doi.org/10.1890/11-0542.1

Lafage, D., Secondi, J., Georges, A., Bouzillé, J.-B., & Pétillon, J. (2014). Satellite-derived vegetation indices as surrogate of species richness and abundance of ground beetles in temperate floodplains. *Insect Conservation and Diversity*, *7*, 327–333. https://doi.org/10.1111/icad.12056

Lande, R. (1993). Risks of population extinction from demographic and environmental stochasticity and random catastrophes. *The American Naturalist*, *142*, 911–927. https://doi.org/10.1086/285580

Lassau, S. A., & Hochuli, D. F. (2008). Testing predictions of beetle community patterns derived empirically using remote sensing. *Diversity and Distributions*, *14*, 138–147. https://doi.org/10.1111/j.1472-4642.2007.00438.x

Letten, A. D., Ashcroft, M. B., Keith, D. A., Gollan, J. R., & Ramp, D. (2013). The importance of temporal climate variability for spatial patterns in plant diversity. *Ecography*, *36*, 1341–1349. https://doi.org/10.1111/j.1600-0587.2013.00346.x

Oliveira, B. F., Machac, A., Costa, G. C., Brooks, T. M., Davidson, A. D., Rondinini, C., & Graham, C. H. (2016). Species and functional diversity accumulate differently in mammals. *Global Ecology and Biogeography*, *25*, 1190–1130. https://doi.org/10.1111/geb.12471

Ovaskainen, O., & Meerson, B. (2010). Stochastic models of population extinction. *Trends in Ecology and Evolution*, *25*, 643–652. https://doi.org/10.1016/j.tree.2010.07.009

Peres-Neto, P. R., Legendre, P., Dray, S., & Borcard, D. (2006). Variation partitioning of species data matrices: Estimation and comparison of fractions. *Ecology*, *87*, 2614–2625. https://doi.org/10.1890/0012-9658(2006)87[2614:VPOSDM]2.0.CO;2

Poff, N. L., & Ward, J. V. (1989). Implications of streamflow variability and predictability for lotic community structure: A regional analysis of streamflow patterns. *Canadian Journal of Fisheries and Aquatic Sciences*, *46*, 1805–1818. https://doi.org/10.1139/f89-228

R Development Core Team. (2017). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.

Rabosky, D. L., & Hurlbert, A. H. (2015). Species richness at continental scales is dominated by ecological limits. *The American Naturalist*, *185*, 572–583. https://doi.org/10.1086/680850

Rabosky, D. L., Chang, J., Title, P. O., Cowman, P. F., Sallan, L., Friedman, M., … Alfaro, M. E. (2018). An inverse latitudinal gradient in speciation rate for marine fishes. *Nature*, *559*, 392–395.

Rabosky, D. L., Title, P. O., & Huang, H. (2015). Minimal effects of latitude on present-day speciation rates in New World birds. *Proceedings of the Royal Society B: Biological Sciences*, *282*, 20142889.

Ricklefs, R. E. (2006). Evolutionary diversification and the origin of the diversity–environment relationship. *Ecology*, *87*(sp7), S3–S13. https://doi.org/10.1890/0012-9658(2006)87[3:EDATO O]2.0.CO;2

Schluter, D. (2016). Speciation, ecological opportunity, and latitude. *The American Naturalist*, *187*, 1–18. https://doi.org/10.1086/684193

Šímová, I., & Storch, D. (2017). The enigma of terrestrial primary productivity: Measurements, models, scales and the diversity–productivity relationship. *Ecography*, *40*, 239–252. https://doi.org/10.1111/ecog.02482

Srivastava, D. S., & Lawton, J. H. (1998). Why more productive sites have more species: An experimental test of theory using tree-hole communities. *The American Naturalist*, *152*, 510–529. https://doi.org/10.1086/286187

Steel, E. A., & Lange, I. A. (2007). Using wavelet analysis to detect changes in water temperature regimes at multiple scales: Effects of multi-purpose dams in the Willamette River basin. *River Research and Applications*, *23*, 351–359. https://doi.org/10.1002/rra.985

Storch, D. (2012). Biodiversity and its energetic and thermal controls. In R. M. Sibly, J. H. Brown, & A. Kodric-Brown (Eds.), *Metabolic ecology: A scaling approach* (pp. 120–131). Oxford, UK: Wiley-Blackwell.

Storch, D., & Okie, J. (2019). The carrying capacity for species richness. *Global Ecology and Biogeography*. https://doi.org/10.1111/geb.12987

Storch, D., Bohdalková, E., & Okie, J. (2018). The more-individuals hypothesis revisited: The role of community abundance in species richness regulation and the productivity–diversity relationship. *Ecology Letters*, *21*, 920–937. https://doi.org/10.1111/ele.12941

Tonkin, J. D., Bogan, M. T., Bonada, N., Rios-Touma, B., & Lytle, D. A. (2017). Seasonality and predictability shape temporal species diversity. *Ecology*, *98*, 1201–1216. https://doi.org/10.1002/ecy.1761

Varpe, Ø. (2017). Life history adaptations to seasonality. *Integrative and Comparative Biology*, *57*, 943–960. https://doi.org/10.1093/icb/icx123

Wiens, J. J., & Donoghue, M. J. (2004). Historical biogeography, ecology and species richness. *Trends in Ecology and Evolution*, *19*, 639–644. https://doi.org/10.1016/j.tree.2004.09.011

Williams, C. M., Ragland, G. J., Betini, G., Buckley, L. B., Cheviron, Z. A., Donohue, K., … Visser, M. E. (2017). Understanding evolutionary impacts of seasonality: An introduction to the symposium. *Integrative and Comparative Biology*, *57*, 921–933. https://doi.org/10.1093/icb/icx122

Wright, D. H. (1983). Species-energy theory: An extension of species-area theory. *Oikos*, *41*, 496–506. https://doi.org/10.2307/3544109

Wright, D. H., Currie, D. J., & Maurer, B. A. (1993). Energy supply and patterns of species richness on local and regional scales. In R. E. Ricklefs, & D. Schluter (Eds.), *Species diversity in ecological communities* (pp. 66–74). Chicago, IL: University of Chicago Press.

BIOSKETCHES

Anna Tószögyová is a doctoral student whose research focuses on macroecological patterns in species and trait diversity.

David Storch is interested in macroecology and ecological theory, with a particular focus on spatial diversity patterns, geometry of species distributions and diversity dynamics.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

How to cite this article: Toszogyova A, Storch D. Global diversity patterns are modulated by temporal fluctuations in primary productivity. *Global Ecol Biogeogr.* 2019;00:1–12. https://doi.org/10.1111/geb.12997

Figure S1

Relationship between species richness in birds (top) and amphibians (bottom) and mean productivity (a), seasonality (b), and unpredictability (c), respectively.

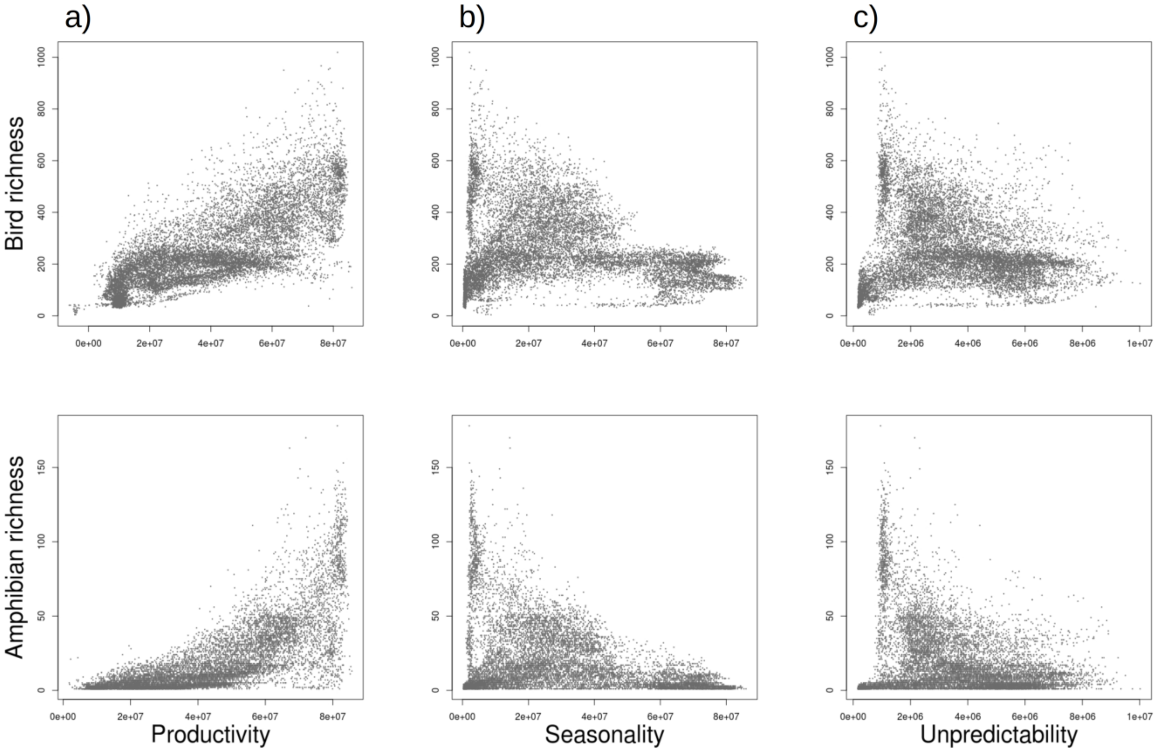
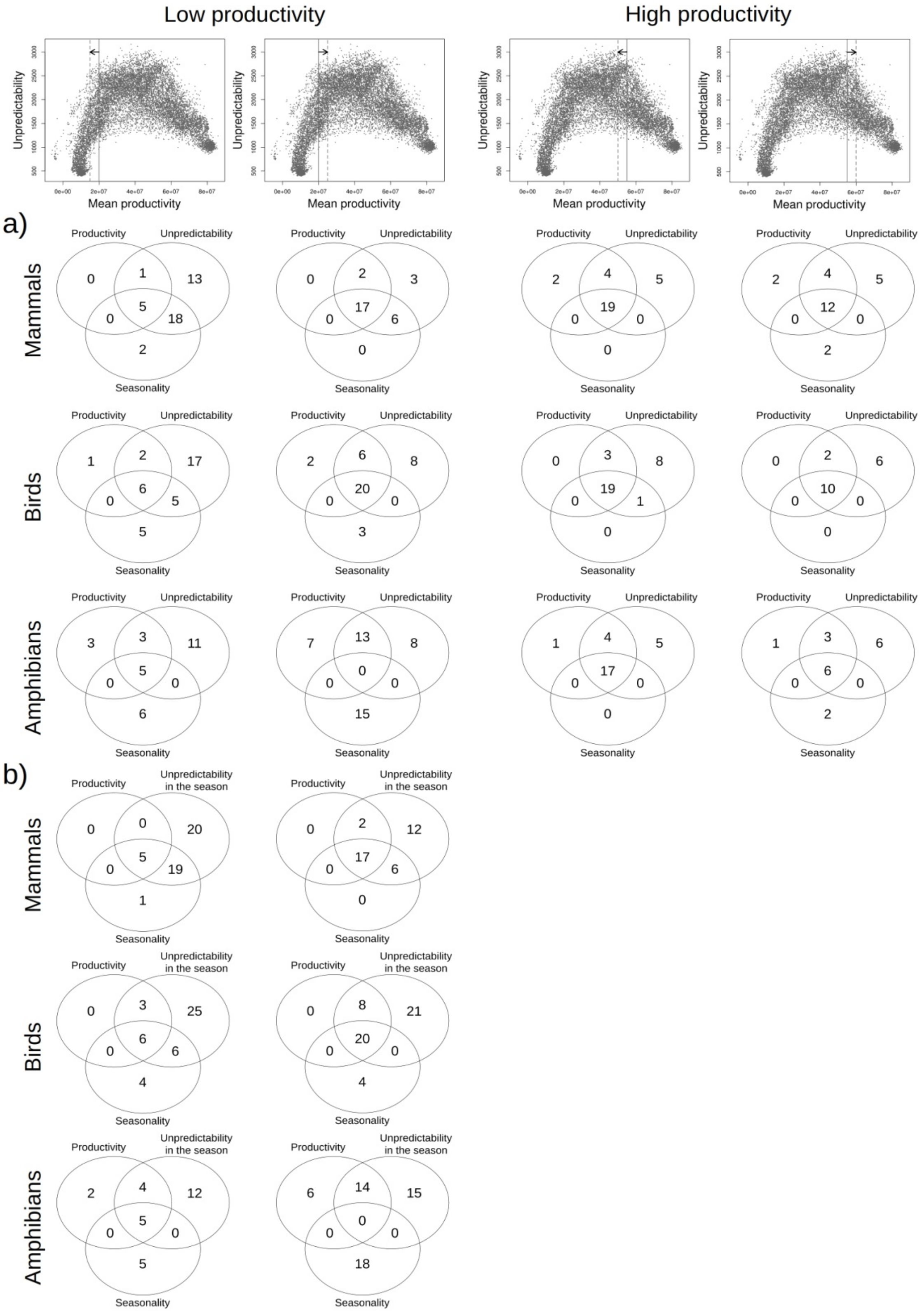


Figure S2

(a) Venn diagrams describing variation partitioning for species richness of mammals, birds and amphibians by mean productivity and productivity seasonality and unpredictability in low- and high-productive regions when the lines dividing the regions were shifted in both directions (above). (b) Variation partitioning for species richness of mammals, birds and amphibians by mean productivity and its seasonality and unpredictability in the productive season in low-productive regions when the lines dividing the regions were shifted in both directions. The diagrams show adjusted R^2 (rounded) values associated with each partition or for overlapping partitions. Unpredictability, especially during the productive season in the case of arid regions, was the strongest predictor of species richness (except that of amphibians in more broadly defined arid areas). Narrowing the delimitation of arid areas increased the effect of unpredictability on species richness.



Appendix S1 List of all explored variables concerning productivity and its variation

The first four variables were used in the final analyses. The other variables were also tested for their effects on species richness, but they were not as strong as the first four variables or they did not show any pronounced spatial patterns.

- *mean productivity* as the mean NDVI value of the time-series data (or the seasonal cycle)
- *seasonality* as the difference between the maximum and minimum of the seasonal cycle
- *unpredictability* as the standard deviation of residuals from the seasonal trend
- *unpredictability in the season* as the standard deviation of residuals from the three on average most productive months
- *unpredictability outside the season* as the standard deviation of residuals from the three on average least productive months
- *intra-annual inconstancy in variability* as the maximum difference in standard deviations of residuals from mean values for each month
- ratio of sd of positive to sd of negative residuals from the three most productive months
- skewness of residuals from the three most productive months
- ratio of sd of positive to sd of negative residuals from the three least productive months
- skewness of residuals from the three least productive months
- *inter-annual variability in means* as the standard deviation of annual means
- *inter-annual variability in maxima* as the standard deviation of annual maxima
- *inter-annual variability in minima* as the standard deviation of annual minima
- coefficient of variation of annual means
- coefficient of variation of annual maxima
- coefficient of variation of annual minima
- *symmetry in variability* as the skewness of residuals from the seasonal trend
- kurtosis of residuals from the seasonal trend
- standard deviation of the smoothed trend after removing the seasonal trend
- coefficient of variation of the smoothed trend after removing the seasonal trend
- range of the smoothed trend after removing the seasonal trend
- *continuous change* as variability in time-series data explained by the linear trend (coefficient of determination)
- *predictability* as the variability in the time-series data explained by the seasonal trend
- *duration of the season* as the number of months when productivity values exceeded 75% of mean maximum productivity

Table S1

Results from the linear regression models testing the relationship between species richness and the given environmental variable after removing the effects of the other environmental variables (a) in the low, medium and high productivity region, respectively, and (b) in the low productivity region where unpredictability in the productive season was considered. We do not put here p-values, since these do not make sense for such high number of spatially autocorrelated data points. For the significance of the most important predictors after accounting for spatial autocorrelation see Table S2. The low size of the coefficients is due to a large difference in the scale of variables.

a)			Estimate	Standard error	t-value	Variance
Low productivity	Mammals	Productivity	2.74 x 10^{-8}	0.95 x 10^{-8}	2.90	0.2%
		Seasonality	-30.62 x 10^{-2}	9.78 x 10^{-2}	-3.13	0.3%
		Unpredictability	201.52 x 10^{-2}	14.08 x 10^{-2}	14.31	6.4%
	Birds	Productivity	1.30 x 10^{-8}	0.16 x 10^{-8}	8.05	2.1%
		Seasonality	-17.65 x 10^{-2}	1.66 x 10^{-2}	-10.65	3.6%
		Unpredictability	46.00 x 10^{-2}	2.36 x 10^{-2}	19.46	11.2%
	Amphibians	Productivity	3.03 x 10^{-8}	0.30 x 10^{-8}	10.25	5.4%
		Seasonality	-39.69 x 10^{-2}	2.69 x 10^{-2}	-14.76	10.7%
		Unpredictability	55.49 x 10^{-2}	4.08 x 10^{-2}	13.59	9.2%
Medium productivity	Mammals	Productivity	7.74 x 10^{-8}	0.21 x 10^{-8}	37.13	18.9%
		Seasonality	-59.16 x 10^{-2}	8.81 x 10^{-2}	-6.72	0.7%
		Unpredictability	-242.48 x 10^{-2}	16.19 x 10^{-2}	-14.98	3.6%
	Birds	Productivity	0.90 x 10^{-8}	0.02 x 10^{-8}	45.61	26.1%
		Seasonality	-14.40 x 10^{-2}	0.85 x 10^{-2}	-16.86	4.6%
		Unpredictability	-26.72 x 10^{-2}	1.59 x 10^{-2}	-16.76	4.5%
	Amphibians	Productivity	2.78 x 10^{-8}	0.04 x 10^{-8}	63.80	41.2%
		Seasonality	-65.87 x 10^{-2}	1.97 x 10^{-2}	-33.44	16.2%
		Unpredictability	-24.56 x 10^{-2}	4.00 x 10^{-2}	-6.14	0.6%
High productivity	Mammals	Productivity	6.98 x 10^{-8}	0.88 x 10^{-8}	7.91	1.6%
		Seasonality	111.59 x 10^{-2}	19.46 x 10^{-2}	5.74	0.9%
		Unpredictability	-453.11 x 10^{-2}	30.73 x 10^{-2}	-14.75	5.5%
	Birds	Productivity	0.15 x 10^{-8}	0.06 x 10^{-8}	2.55	0.1%
		Seasonality	3.58 x 10^{-2}	1.30 x 10^{-2}	2.75	0.2%
		Unpredictability	-34.74 x 10^{-2}	2.03 x 10^{-2}	-17.15	7.3%
	Amphibians	Productivity	0.67 x 10^{-8}	0.12 x 10^{-8}	5.65	0.8%
		Seasonality	15.47 x 10^{-2}	2.59 x 10^{-2}	5.97	0.9%
		Unpredictability	-60.82 x 10^{-2}	4.11 x 10^{-2}	-14.79	5.5%
b)						
Low productivity	Mammals	Productivity	-0.64 x 10^{-8}	0.97 x 10^{-8}	-0.67	-0.02%
		Seasonality	-21.83 x 10^{-2}	7.17 x10^{-2}	-3.05	0.3%
		Unpredictability in the season	228.15 x 10^{-2}	10.00 x 10^{-2}	22.81	14.8%
	Birds	Productivity	0.64 x 10^{-8}	0.17 x 10^{-8}	3.87	0.5%
		Seasonality	-14.06 x 10^{-2}	1.21 x 10^{-2}	-11.61	4.3%
		Unpredictability in the season	48.71 x 10^{-2}	1.64 x 10^{-2}	29.66	22.7%
	Amphibians	Productivity	2.85 x 10^{-8}	0.29 x 10^{-8}	9.69	4.9%
		Seasonality	-33.32 x 10^{-2}	2.15 x 10^{-2}	-15.48	11.7%
		Unpredictability in the season	50.10 x 10^{-2}	3.01 x 10^{-2}	16.62	13.2%

Table S2

Results from the spatial generalized least squares models (accounting for spatial autocorrelation) testing the relationship between species richness and the strongest environmental variable (after accounting for the effect of the other variables) for a given taxa and region. In low productivity regions, unpredictability in the productive season was even stronger predictor of species richness than year-round unpredictability. For amphibians in low productivity regions, seasonality was the strongest predictor, but after accounting for space it was not significant. The low size of the coefficients is due to a large difference in the scale of variables.

			Estimate	Standard error	t-value	p-value
Mammals	Low productivity	Unpredictability	63.90 x 10^{-2}	8.34 x 10^{-2}	7.66	0
		Unpredictability in the season	33.33 x 10^{-2}	6.26 x 10^{-2}	5.32	0
	Medium productivity	Productivity	2.35 x 10^{-8}	0.13 x 10^{-8}	18.50	0
	High productivity	Unpredictability	-66.31 x 10^{-2}	14.36 x 10^{-2}	-4.62	0
Birds	Low productivity	Unpredictability	7.31 x 10^{-2}	1.16 x 10^{-2}	6.31	0
		Unpredictability in the season	2.59 x 10^{-2}	0.87 x 10^{-2}	3.00	0.0028
	Medium productivity	Productivity	0.26 x 10^{-8}	0.01 x 10^{-8}	21.54	0
	High productivity	Unpredictability	-8.69 x 10^{-2}	1.11 x 10^{-2}	-7.81	0
Amphibians	Low productivity	Seasonality	4.01 x 10^{-2}	3.63 x 10^{-2}	1.1	0.27
		Unpredictability	14.15 x 10^{-2}	4.41 x 10^{-2}	3.21	0.0014
		Unpredictability in the season	7.37 x 10^{-2}	3.27 x 10^{-2}	2.25	0.024
	Medium productivity	Productivity	0.68 x 10^{-8}	0.03 x 10^{-8}	19.61	0
	High productivity	Unpredictability	-14.91 x 10^{-2}	2.96 x 10^{-2}	-5.04	0

Chapter 4

Female solo song and duetting are associated with different territoriality in songbirds

Running head: Ecology of female birdsong

Peter Mikula[1,2*], Anna Tószögyová[3,4], David Hořák[3], Tereza Petrusková[3], David Storch[3,4], Tomáš Albrecht[1,2]

[1]Department of Zoology, Faculty of Science, Charles University, Viničná 7, 128 44 Prague 2, Czech Republic; E-mail: petomikula158@gmail.com

[2]Institute of Vertebrate Biology, Czech Academy of Sciences, Květná 8, 603 65 Brno, Czech Republic; E-mail: albrecht@ivb.cz

[3]Department of Ecology, Faculty of Science, Charles University, Viničná 7, 128 43 Prague 2, Czech Republic; E-mail: david.horak@natur.cuni.cz, kumstatova@post.cz

[4]Center for Theoretical Study, Charles University and the Czech Academy of Sciences, Jilská 1, 110 00 Prague 1, Czech Republic; E-mail: anna83@seznam.cz, storch@cts.cuni.cz

[4]Institute of Vertebrate Biology, Czech Academy of Sciences, Květná 8, 603 65 Brno, Czech Republic; E-mail: albrecht@ivb.cz

*Author for correspondence: ORCID: 0000-0002-2731-9105

https://doi.org/10.5061/dryad.fn2z34tpr

Abstract

Recently, there has been an increased effort to unravel selective factors behind female song evolution in songbirds. Female birds which produce songs may sing either solo or in duets; although the two vocal performances likely evolved through different selection forces and mechanisms, the majority of large-scale studies to date have focused only on duetting or female song in general (pooling female solo song and duetting into a single category). Hence, here we estimate the effect of behavioral life-history traits (territoriality, social bonds, cooperative breeding) and environmental productivity on the occurrence of female solo song and duetting separately in songbirds of South Africa and Lesotho. The focal region is characterized by subtropical/tropical climate, clear spatial environmental productivity gradient, and detailed knowledge on avian species distribution and behavioral life-history traits. Phylogenetically informed comparative analyses revealed that species where females produce only solo songs exhibited higher levels of territoriality than species with non-singing females (in an univariable model) but, simultaneously, lower levels than duetting species. Although both species with female solo song and duetting establish mainly long-term social bonds, the former defend their territories seasonally while the latter exhibit mainly year-round territoriality. Cooperative breeding and environmental productivity was not associated with the distribution of female solo song and duetting in any model. Our results indicate that when exploring female song ecology and evolution, female solo song and duetting are likely to be distinct song categories associated with different levels of territoriality.

Keywords: behavioral life-history traits, macroecology, normalized difference vegetation index, phylogenetic comparative analyses

Introduction

The complex song of songbirds (Passeriformes: Passeri) have long been attributed to males only, with the assumption that it evolved through sexual selection via male–male competition and female choice (Darwin 1871; Catchpole 1987). Present opinion is that female song is ancestral to songbirds and that it is phylogenetically widespread and occurs in species inhabiting a range of climatic zones (Garamszegi et al. 2007; Odom et al. 2014). In general, females may sing either independently of males, i.e. emitting solo songs, or in duets, i.e. coordinated with the mate. For species in which both sexes sing, the prevailing view is that females sing for similar reasons as males (but the distribution of functions of female song could to be more variable than in males) (Langmore 1998; Hall 2004). In addition to intra-pair contact (de Silva et al. 2004) and coordination of breeding activities (Gilbert and Carroll 1999), female singing may also be associated with mate attraction, mate guarding and defense of territories (Langmore 1998; Hall 2004, 2009; Cain and Langmore 2015; Krieg and Getty 2016; Tobias et al. 2016). Although female solo song and duetting can share some similar functions, the two types of performances are not necessarily equivalent (Langmore 1998; Hall 2009; Odom et al. 2015; Tobias et al. 2016). Moreover, while duets are rare in temperate zone birds, female solo song occurs more often there than duetting (Garamszegi et al. 2007; Tobias et al. 2016). Differences in function and geographical distribution between these two types of vocal performance indicate that they likely evolved through different selection forces and mechanisms (Odom et al. 2015).

Previous studies have shown an association between the distribution of female song in general (involving both duetting and female solo song) and behavioral life-history traits such as the long-term territoriality (Robinson 1948; Benedict 2008), occurrence of social monogamy (Price 2009; Odom et al. 2015; but see Benedict 2008), absence of migration (Price 2009; Odom et al. 2015; Logue and Hall 2014), and convergent sex-roles (Slater and Mann 2004). A global synthesis on social and environmental factors behind the evolution of duetting revealed that duetting was, out of many factors evaluated, most strongly linked to year-round territoriality and stable social bonds (Tobias et al. 2016). Nevertheless, it is difficult to make a deeper insight into female solo song evolution from these studies, because results in female song studies might be largely driven by the inclusion of duetting species. Evolutionary and ecological factors driving the evolution of female solo song remain largely unexplored and large-scale studies on female solo song are, according to our best knowledge, still missing. For instance, it is unclear which selective factors favor the evolution of female solo song and duetting with respect to each other.

Global variation in avian behavioral traits, as, for instance, territoriality (Maher and Lott 2000), breeding systems (Jetz and Rubenstein 2011), and migration (Alerstam et al. 2003), is largely determined by environmental conditions including those presumably associated with the distribution of female song evolution. Species with females that sing are predicted to inhabit regions with high resource availability and little seasonal change. Such birds are expected to reside and breed over the prolonged season (Ricklefs 1969; Price et al. 2009) and experience increased pressure from both intra- and inter-specific intruders (Ballance et al. 1997; Justino et al. 2012). In fact, predictable environments rich in food resources seem to favor birds exhibiting more sedentary lifestyles and longer-term partnerships, thus driving the evolution of singing in female birds (Logue and Hall 2004; Odom et al. 2015; Tobias et al. 2016). Indeed, species with females that sing have been found to be particularly common among highly productive tropical regions characterized by low levels of environmental seasonality (Morton 1996; Slater and Mann 2004; Price et al. 2009; Odom et al. 2014, 2015; Tobias et al. 2016).

In this study, we employed phylogenetic comparative analyses to explore interspecific variability in female solo song and duetting in association to important intrinsic (behavioral) and extrinsic (environmental productivity across species distribution range) traits in songbirds to determine if both vocal performances are associated with the same or different selective factors. First, we explored variability in duetting, because a substantial body of theoretical and empirical work regarding female song ecology and evolution focuses on duetting, and predict that females that sing in duets belong mainly to species with year-round territoriality, establishing long-term social bonds as well as inhabiting more productive areas (Tobias et al. 2016). However, female solo song seems to be relatively more common than duetting in temperate zone species (Garamszegi et al. 2007; Odom et al. 2015) which exhibit different behavioral traits and face more variable environment; hence, we predict associations of female solo song with decreased level of territoriality, shorter-term social bonds and lower environmental productivity compared to duetting species. We tested these hypotheses on a sample of songbirds breeding in sub-Saharan Africa that is rarely studied in regards to avian female song. We specifically focused on South Africa and Lesotho, a region occupied by more than 350 songbird species of 39 families (Lepage 2018). The knowledge on species distribution, life-histories and environmental conditions is exceptionally detailed there (see methods), making the region very well suited for our research purposes. From a global perspective, South African songbirds typically exhibit slow (“tropical”) pace of life (Jetz et al. 2008), but on regional scale these traits tend to vary across species, and species in the region significantly differ in production of female song (Hockey et al. 2005). Furthermore, while the climate is generally subtropical to tropical, key environmental conditions in the region show a clear longitudinal trend (driven by a longitudinal precipitation gradient), from dry and unproductive desert in the west to moist and productive woodland in the east (Hořák et al. 2015).

Methods

Data Collection

Species distribution data

Comprehensive data on the distribution of songbird species across South Africa and Lesotho were obtained from the Southern African Bird Atlas Project (SABAP) (Harrison et al. 1997), which surveyed all birds living in this region between 1987 and 1992. Each set of songbird species recorded within a fine ~25 × 25 km grid cell (0.25° spatial resolution) was considered as a local assemblage (the region covered by 1,858 grid cells/assemblages in total).

Female song data collection

Song was defined as primary long-range complex acoustic vocalization used by birds mainly during the breeding season. In accordance with this definition, information on the presence or absence of female song in South African songbirds was primarily obtained from data compiled for global assessments, with further relevant data taken from other literature sources (see below for further details). Species producing only simple call-like vocalization (e.g. some corvids) were omitted from the analyses because the lack of song in both sexes might be because of different selection pressures than in species with male song only. Similarly, species for which relevant information on vocalization was lacking were omitted from further analyses.

Duetting dataset: Duetting was defined as coordinated or alternated long-range vocalization that is performed communally by two bird individuals (usually the members of a mated pair) (Tobias et al. 2016). This working definition harbors duets as generally understood, but excludes simple vocalizations such as different types of calls. Following suggestions by Logue and Hall (2014) and Tobias et al. (2016), duetting species were pooled together with chorusing species (involving three or more individuals), because both types of signalizations are similar in structure and function (Logue and Hall 2014). It is thus often difficult to distinguish between them (e.g. many duetting species were observed chorusing and vice versa) and, moreover, duets and choruses are thought to have evolved under similar selection pressures (e.g. Seddon and Tobias 2003; Tobias et al. 2016).

Female solo song dataset: Because information that females of particular species sing only solo songs is rarely explicitly stated in literature, we have to extract such information by focusing on indirect evidence. Firstly, we prepared a female song dataset where we combined data on presence/absence of female song in general provided by Webb et al. (2016), then Hockey et al. (2005), which directly focus on birds of South Africa and Lesotho, and finally continuously updated online edition of "Handbook of the Birds of the World Alive" (del Hoyo et al. 2016). In general, female song was scored as present when females were reported as singing or where species accounts stated that song is persistent in both sexes. Female song was scored as absent when production of song was reported by males only, or when female produced only simple calls. Finally, scores on female solo song distribution among species were obtained by combination of data included in female song and duetting dataset. We considered that a given species only has a female solo song if female song was scored as present for that species in the female song dataset and simultaneously the exhaustive update on duetting distribution across world birds by Tobias et al. (2016) stated that females of this species do not sing in duets or choruses.

After excluding temperate zone migrants (13 species) and species lacking information on all traits (nine species), of the 278 songbird species for which we had breeding distributional data, we were able to obtain information on presence/absence of duetting for 269 species (out of these 52 species produce duets) and presence/absence of female song for 163 species (out of these 30 species produce female solo song).

Behavioral life-history traits

We collected data on several key behavioral life-history traits hypothesized to play a role in the evolution of song production in female songbirds, including the level of territoriality, stability of social bonds, and cooperative breeding (Logue and Hall 2014; Najar and Benedict 2015; Odom et al. 2015; Tobias et al. 2016). Information on these traits for species breeding in South Africa and Lesotho were obtained from recent large-data compilations by Tobias et al. (2016) (territoriality and social bond type) and Dale et al. (2015) (cooperative breeding). Tobias et al. (2016) also scored data according to the level of quality (i.e. uncertainty of classification assignment). The majority of data on territoriality and social bond for birds of South Africa were of high quality; we thus decided to omit quality scores from the analysis. Because definitions and categories in some traits change from source to source, we provide definitions as used in data-source studies.

Territoriality: Species were scored following definitions provided by Tobias et al (2016) as follows: (1) non-territorial that do not defend territories, or defend only very small areas around nest sites, or species where males defend song or display posts only; (2) seasonally or weakly territorial, having home ranges that largely overlap, or that usually join mixed flocks with poorly defined spatial ranges; and (3) year-round territorial that defend territories all year (for further details see Tobias et al. 2016).

Social bonds: Species were scored as (1) solitary if they do not form pairs, or form them only for a short time during the courtship period, (2) having short-term pair/group bonds if they establish only seasonal partnership and change it in subsequent breeding attempts (low partner fidelity and >50% divorce rate per year), and (3) having long-term pair/group bonds if pair/group members establish year-round partnership or their seasonal pair/group lasts toward subsequent breeding attempts (high partner fidelity and <50% divorce rate per year) (for further details see Tobias et al. 2016).

Cooperative breeding: Species were classified in the following way: (1) non-cooperative; species with no more than two adult birds caring for the offspring, and (2) cooperative; species with more than two birds taking care for the offspring (for further details see Dale et al. 2015).

Environmental productivity

We obtained the ‘normalized difference vegetation index’ (hereafter NDVI), an estimate of environmental productivity based on the spectral properties of vegetation, for each grid cell from the data set provided by the U.S. Geological Survey (http://iridl.ldeo.columbia.edu/SOURCES/.USGS/.ADDS). Maximum NDVI values (hereafter $\mathrm{NDVI}_{\mathrm{max}}$), represented by the average NDVI value of the month with the highest NDVI (available for 1981–2008), were chosen as a proxy of environmental productivity. As the NDVI describes the ‘greenness’ of vegetation, and is closely correlated with rainfall, total green biomass and net primary productivity (Goward and Dye 1987; Chong et al. 1993; Paruelo et al. 1997; Schmidt and Karnieli 2002), it is expected to reflect food availability to songbirds. This assumption is supported by the findings of Lassau and Hochuli (2008) and Lafage et al. (2014), who found a positive correlation between the amount of food available (e.g. arthropod abundance) in the breeding season and NDVI. For subsequent statistical analyses concerning individual species, we calculated the average values of $NDVI_{max}$ across all cells occupied by given species. We used $NDVI_{max}$ because we expected that the analysed traits could play an important role during a breeding period, typically a period of the year when birds can potentially obtain the maximum amount of food resources from the environment.

Phylogenetic tree construction

A phylogenetic tree of South African songbirds was constructed using the avian phylogenetic tool available at http://birdtree.org/ (Jetz et al. 2012). The maximum credibility tree was built from 1000 randomly generated trees based on a Hackett backbone (Hackett et al. 2008). Moreover, for subsequent analyses we also used 100 randomly selected phylogenetic trees. The maximum clade credibility tree was then determined using the TreeAnnotator tool v. 1.8.2 in the BEAST software package v. 1.8.2 (Drummond and Rambaut 2007).

Statistical analyses

As phylogenetically related taxa have a higher probability of sharing characteristics from a common ancestor, phylogenetic relatedness of species could affect presence of duetting and female solo song. Therefore, we modeled associations between variables, including non-independence in species data, using phylogenetic generalized linear mixed-effect models (PGLMM) (Ives and Helmus 2011). We produced models containing all behavioral life-history traits and environmental productivity as explanatory variables, and with duetting and female solo song as a response variables. Duetting, female solo song, and cooperative breeding were used as binary (presence/absence) variables, while environmental productivity was used as a continuous variable. We decided to use territoriality and social bonds as continuous rather than categorical variables in the analyses because there is a gradient in the levels of these variables, which means that the cut-off criteria for their categorization into distinct categories were somewhat arbitrary. Moreover, models with continuous variables are less sensitive to available sample size and the symmetry of the observations for each category. It should be noted, however, that inclusion of territoriality and social bonds as categorical explanatory variables did not change the overall conclusions (see below, and Tables S6–S7).

We performed four comparisons contrasting: (1) duetting species and non-duetting species (with either non-singing and solo singing females), (2) duetting species and species with non-singing females, (3) species with females producing solo song and duetting species, and (4) species with females producing solo song and species with non-singing females. First, we conducted a multivariable model and subsequently univariable models for each explanatory variable separately (for univariable models see Table S1). We used species-level phylogeny; to enhance the informative value of results, we used two ways how to deal with phylogenetic uncertainty. In one case we performed a model with single maximum credibility phylogenetic tree, and in the second case we used 100 randomly selected phylogenetic trees and combined the outputs as the average values of the posterior outcomes (Table S2). These two approaches were applied for both multivariable and univariable models, respectively, and showed the same results; hence, in the main text, we report only models using single maximum credibility phylogenetic tree. However, because every species was represented by only one sample in our dataset, the random effect of the species could potentially be confounded with the residuals (Hadfield 2010a). To avoid this obstacle and test the robustness of these results, we also performed the same models with different parameterization using family-level phylogeny (Tables S3–S5); importantly, both approaches gave identical results.

We performed PGLMM by Bayesian inference using the Markov chain Monte Carlo technique (MCMCglmm; Hadfield 2010b). This approach allowed us to control for phylogenetic co-variation among species by including phylogenetic distance into the model as a random variable (Hadfield and Nakagawa 2010). We used the inverse-gamma prior for random effects and an uninformative prior for the residual variance in all MCMCglmms. The choice of priors was determined by the character of our data, sometimes containing a small number of samples for some variable categories. All models were run for 1,000,000 iterations with elimination of the first 20,000 iterations as a burn-in period and thinning to every 100th iteration. All binary variables were centered by subtracting their mean and the numeric variables were centered and standardized on the same scale (range 1) to improve interpretability. For models with a maximum credibility phylogenetic tree, we used the Gelman-Rubin statistic to check convergence of multiple MCMC chains runs in parallel. This compares within-chain variance to between-chain variance and calculates the potential scale reduction factor (Gelman and Rubin 1992). The iteration chains mixed well, exhibiting no observable autocorrelation. The Gelman-Rubin statistic threshold for models with a maximum credibility phylogenetic tree was < 1.05 in all models. Posterior fixed effect distribution was examined for overlap with zero (as the significance test), using 95% highest posterior density as a credible interval. We also calculated phylogenetic signal as an estimate of the proportion of variance in duetting and female solo song after conditioning on explanatory variables explained by the effect of phylogenetic relatedness. All data were processed and statistically analyzed using R 3.3.1 (R Development Team 2016).

Results

We found that in the first two comparisons, i.e. duetting species vs. non-duetting species, and duetting species vs. species with non-singing females, the strongest predictors of duetting distribution was the level of territoriality and length of social bonds. However, it was not possible to test the effect of social bonds in these contrasts as it was not possible to estimate the posteriors for this parameter. This was because all species singing in duets fall into one category of social bonds (long-term). This, however, indicates that the association of duetting song with the long-term social bonds is indeed strong. Univariable models lead to the same results (Fig. 1, Table 1, see also Tables S1–S2). Species where females sing in duets maintain longer-term territoriality and social bonds when compared with relatively shorter-term territoriality and social bonds in species where females produce no duets and no female song, respectively. However, when contrasting species with females singing solo songs and duetting species, the only statistically significant association in both multivariable and univariable models was with the level of territoriality such that the level of territoriality increases toward duetting species (Fig. 1, Table 1, see also Tables S1–S2). Finally, when contrasting species with female solo song and species with non-singing females no significant predictor was identified in multivariable models. However, univariable models revealed association with the level of territoriality; species wherein females produce solo songs exhibited higher level of territoriality than species with no female song (Fig. 1, Table 1, see also Tables S1–S2). In all contrasts, cooperative breeding and the environmental variable, NDVI_{max}, did not explain the presence of any singing characteristic.

To test robustness of these results, we also prepared models where territoriality and social bonds were coded as categorical variables (results are summarized in Tables S6–S7). Duetting species exhibited significantly more often year-round territoriality than seasonal or weak territoriality when compared with non-duetting species and species with no female song. Furthermore, species with solo singing females were significantly more often seasonally territorial when compared with mainly year-round territorial duetting species but exhibited lower proportion of weak territoriality than species with no female song.

The above results are nicely supported by spatial geographical patterns. There was a clear spatial pattern in duetting distribution across the study region (Fig. 2a, b), where regions with a high proportion of duetting songbirds strongly overlapped spatially with regions with high proportion of year-round territorial species (Fig. S1). At the same time, the association between the proportion of duetting and environment (NDVI_{max}) was less clear; however, higher proportion of duetting species was partially recorded in humid and highly productive areas (Fig. S1), including savannahs, woodlands and forests in eastern and north-eastern South Africa, as well as areas along the Indian Ocean coastline. A low proportion (occasionally approaching zero) of duetting species was detected in central, higher elevated grasslands, and in Succulent Karoo, Nama Karoo, and Kalahari and Namib Deserts in western South Africa. When contrasting species with the presence of female solo song against species with the presence of duetting, the proportion of female solo song was highest in central parts of South Africa (Fig. 2c), copying geographical trends in the distribution of seasonal territoriality; these areas were also characterized by less productive environments (Fig. S1). Finally, when contrasting species with the presence of female solo song against species without female song, areas with the high proportion of species with female solo song geographically coincides with areas with the high proportion of year-round territorial species, similarly to the first two previous contrasts (duetting vs. non-duetting and duetting vs. no female song; Fig. 2d, Fig. S1).

Discussion

We found high variation among South African songbirds with regard to the presence of female singing. It is worth noting that species involved in our study exhibit slow pace of life from a global perspective (Jetz et al. 2008), and inhabit subtropical to tropical environments, where singing females are often reported (Tobias et al. 2016). Although both duetting species and species with female solo song establish mainly long-term social bonds, female solo song–duetting comparison revealed a negative association between presence of female solo song and territoriality. Subsequent analysis found that duetting species exhibited mainly the year-round territoriality while female solo song predominated in species that are territorial only seasonally although the proportion of year-round territorial species was still relatively high (>20%) in latter group. Species wherein females do not produce song exhibited on average lower level of territoriality than species with solo singing (in univariable model only) and duetting females. Interestingly, neither in multivariable models nor in univariable models cooperative breeding and environmental productivity was associated with the distribution of duetting and female solo song. Hence, level of territoriality rather than other social and environmental factors is the immediate driver affecting the distribution of female song performances in our sample of subtropical to tropical birds.

We found that female solo song emerged mainly in species exhibiting seasonal territoriality while duetting species were characterized by the presence of year-round territoriality. This indicates that the two vocal performances probably evolved in association with different selection pressures or different levels of the selection factors (Langmore 1998). Price (2015) suggested that sexual dimorphism in singing is often the result of losses in females rather than gains in males. Then, instead of being an evolutionary precursor of duetting, presence of female solo song may also emerge in bird lineages which expanded to areas where year-round territoriality is costly, e.g. from tropical to temperate zones. However, further studies are needed to focus in greater detail on factors and large-scale patterns of female solo song in birds. Either way, despite the fact that duetting and female solo song are often clumped together under the "female song" category in multitaxonomic studies (e.g. Najar and Benedict 2015; Webb et al. 2016), our results suggest that the two vocal performances should be considered as independent composites of female song (also see Odom et al. 2015).

Although it is difficult to disentangle effects of territoriality and social bonds on duetting, it seems that the presence of duetting is more closely associated with presence of year-round territoriality than presence of long-term social bonds (though this was not explicitly tested; also see Tobias et al. 2016). We argue that although the presence of duetting is slightly better predicted by long-term social bonds than year-round territoriality, absence of duetting was almost always linked to the loss of year-round territoriality while majority of non-duetting species still establish long-term social bonds. For instance, duets were completely lacking in some of species-rich families inhabiting South Africa such as old-world buntings (Emberizidae), finches (Fringillidae), swallows and martins (Hirundinidae) and pipits and wagtails (Motacillidae) with no year-round territorial species, while all batises and wattle-eyes (Platysteiridae) together with bush-shrikes (Malaconotidae) defend their territories year-round and also sing in duets. This close duetting–year-round territoriality association suggest that, similarly to findings of Tobias et al. (2016) on a global scale, variation in duetting among songbirds of South Africa could be explained by uneven taxonomic and geographical distribution of year-round territoriality rather than by other factors.

We found no direct association between distribution of any of female song composites and environmental productivity. Although South Africa represents a relatively small area in terms of a global perspective, the local productivity shows a clear and strong gradient with huge regional differences in $NDVI_{max}$; hence, the lack of this association should not be attributed to only low variation in the environmental variable evaluated. However, social behavior of birds has inevitably evolved in accordance with environmental conditions. For instance, distribution of year-round territoriality coincides to some level with the distribution of highly productive areas in South Africa (Fig. S1). Similarly, an inverse association between NDVI and clutch sizes indicates that South African songbirds inhabiting more productive areas exhibit slower pace of life (Hořák et al. 2015). In productive and relatively stable environments, species can reside and breed over the prolonged season as they are not forced to migrate, promoting sedentary lifestyles and affecting also birds' willingness to defend their territories over long periods (Ricklefs 1969; Price et al. 2009; Odom et al. 2015; Tobias et al. 2016). Under such conditions, source and mate defense may become too demanding, thus promoting singing in both partners (Tobias et al. 2016). Taken from the opposite side, these premises indicate that species inhabiting less productive and more variable environment are expected to exhibit lower levels of territoriality, favoring the presence of female solo song or no song in female birds over duetting. It is also possible that some other unmeasured environmental factor, or more probably a combination of several of them, forms specific conditions facilitating the emergence of duetting. Altogether, our results indicate that the strength of selection favoring year-round territoriality may be spatially variable also within tropical and subtropical regions, such as over the territory of South Africa.

Both female solo song and duetting are associated with higher levels of territoriality and long-term social bonds, suggesting that they may have evolved as by-product of cooperative breeding (Seddon and Tobias 2003). However, we did not find any effect of cooperative breeding neither on female solo song nor on duetting . This may indicate that, at least in our sample of species, the evolution of singing in females and cooperative breeding is independent. Other possibility is that the absence of such association in South African species could be linked to low variability in this trait and presence of cooperative breeding only in few avian clades in the area.

In conclusion, our study finds some evidence that species of South Africa and Lesotho wherein female birds produce solo song exhibited, on average, a lower level of territoriality than duetting species but, simultaneously, a higher level of territoriality than species with non-singing females. Hence, we suggest that female solo song and duetting may represent independent composites of female song whose evolution is driven by different levels of the territoriality. We propose that the actual value of individual territory, and consequently a bird's willingness to defend these territories, are primary drivers of the evolution of female solo song and duetting in South African songbirds. Although our study focuses on a restricted region and limited set of species, our results may have implications for furthering understanding of bird song evolution in general, and female solo song in particular. For instance, it may help to explain why female solo song is more common than duetting in non-tropical (e.g. temperate zone) songbird species.

Acknowledgements

This study was financially supported through the Czech Science Foundation (14–36098G).

We are very thankful to Kevin Roche for valuable comments on previous version of manuscript. The authors declare no competing interests.

Data Accessibility: Analyses reported in this article can be reproduced using the data provided by Mikula et al. (2019).

Author contributions

P.M. and T.A. conceived the research, P.M. and A.T. collected the data, A.T. performed the statistical analysis with contribution of all authors to data interpretation, P.M. with input from T.A. wrote the manuscript, all co-authors contributed to the final version of manuscript.

References

Alerstam TA, Hedenström A, Åkesson S. 2003. Long-distance migration: evolution and determinants. Oikos. 103:247–260.

Ballance LT, Pitman RL, Reilly SB. 1997. Seabird community structure along a productivity gradient: importance of competition and energetic constraint. Ecology. 78:1502–1518.

Benedict L. 2008. Occurrence and life history correlates of vocal duetting in North American passerines. J Avian Biol. 39:57–65.

Cain KE, Langmore NE. 2015. Female and male song rates across breeding stage: testing for sexual and nonsexual functions of female song. Anim Behav. 109:65–71.

Catchpole CK. 1987. Bird song, sexual selection and female choice. Trends Ecol Evol. 2:94–97.

Chong DLS, Mougin E, Gastellu-Etchegorry JP. 1993. Relating the global vegetation index to net primary productivity and actual evapotranspiration over Africa. Int J Remote Sens. 14:1517–1546.

Dale J, Dey CJ, Delhey K, Kempenaers B, Valcu, M. 2015. The effects of life history and sexual selection on male and female plumage colouration. Nature. 527:367.

Darwin C. 1871. The descent of man. London, U.K: J. Murray.

de Silva HG, Marantz CA, Perez-Villafana M. 2004. Song in female *Hylorchilus* wrens. Wilson Bull. 116:186–188.

del Hoyo J, Elliott A, Sargatal J, Christie DA, de Juana E. 2015. Handbook of the birds of the world alive. Barcelona, Spain: Lynx Edicions. Available at http://www.hbw.com/.

Drummond AJ, Rambaut A. 2007. BEAST. Bayesian evolutionary analysis by sampling trees. BMC Evol Biol. 7:214.

Garamszegi LZ, Pavlova DZ, Eens M, Møller AP. 2007. The evolution of song in female birds in Europe. Behav Ecol. 18:86–96.

Gelman A, Rubin DB. 1992. Inference from iterative simulation using multiple sequences. Statist Sci. 7:457–472.

Gilbert WM, Carroll AF. 1999. Singing in a mated female Wilson’s warbler. Wilson Bull. 111:134–137.

Goward SN, Dye DG. 1987. Evaluating North American net primary productivity with satellite observations. Adv Space Res. 7:165–174.

Hackett SJ, Kimball RT, Reddy S, Bowie RCK, Braun EL, Braun MJ, Chojnowski JL, Cox WA, Han KL, Harshman J, Huddleston CJ, Marks BD, Miglia KJ, Moore WS, Sheldon FH, Steadman DW, Witt CC, Yuri T. 2008. A phylogenomic study of birds reveals their evolutionary history. Science. 320:1763–1768.

Hadfield JD. 2010a. MCMCglmm course notes. Available at http://cran.r-project.org/web/packages/MCMCglmm/vignettes/CourseNotes.pdf

Hadfield JD. 2010b. MCMC methods for multi-response generalised linear mixed models: the MCMCglmm R package. J Stat Softw. 33:1–22.

Hadfield JD, Nakagawa S. 2010. General quantitative genetic methods for comparative biology: phylogenies, taxonomies and multi-trait models for continuous and categorical characters. J Evol Biol. 23:494–508.

Hall ML. 2004. A review of hypotheses for the functions of avian duetting. Behav Ecol Sociobiol. 55:415–430.

Hall ML. 2009. A review of vocal duetting in birds. Adv Stud Behav. 40:67–121.

Harrison JA, Allan DG, Underhill LG, Herremans M, Tree AJ, Parker V, Brown CJ. 1997. The atlas of southern African birds. Vol. 2: passerines. Johannesburg, South Africa: BirdLife South Africa.

Hockey PAR, Dean WRJ, Ryan PG. 2005. Roberts – Birds of southern Africa, VIIth ed. Cape Town, South Africa: The Trustees of the John Voelcker Bird Book Fund.

Hořák D, Tószögyová A, Storch D. 2015. Relative food limitation drives geographical clutch size variation in South African passerines: a large-scale test of Ashmole's seasonality hypothesis. Glob Ecol Biogeogr. 24:437–447.

Ives AR, Helmus MR. 2011. Generalized linear mixed models for phylogenetic analyses of community structure. Ecol Monogr. 81:511–525.

Jetz W, Rubenstein DR. 2011. Environmental uncertainty and the global biogeography of cooperative breeding in birds. Curr Biol. 21:72–78.

Jetz W, Sekercioglu CH, Böhning-Gaese K. 2008. The worldwide variation in avian clutch size across species and space. PLoS Biol. 6:e303.

Jetz W, Thomas GH, Joy JB, Hartmann K, Mooers AO. 2012. The global diversity of birds in space and time. Nature. 491:444–448.

Justino DG, Maruyama PK, Oliveira PE. 2012. Floral resource availability and hummingbird territorial behaviour on a Neotropical savanna shrub. J Ornithol. 153:189–197.

Krieg CA, Getty T. 2016. Not just for males: females use song against male and female rivals in a temperate zone songbird. Anim Behav. 113:39–47.

Lafage D, Secondi J, Georges A, Bouzillé J-B, Pétillon J. 2014. Satellite-derived vegetation indices as surrogate of species richness and abundance of ground beetles in temperate floodplains. Insect Conserv Diver. 7:327–333.

Langmore NE. 1998. Functions of duet and solo songs of female birds. Trends Ecol Evol. 13:136–140.

Lassau SA, Hochuli DF. 2008. Testing predictions of beetle community patterns derived empirically using remote sensing. Divers Distrib. 14:138–147.

Lepage D. 2018. Avibase: bird checklists of the world – South Africa. Available at http://avibase.bsc-eoc.org/checklist.jsp?region=za&list=howardmoore. Accessed July 12, 2018.

Logue DM, Hall ML. 2014. Migration and the evolution of duetting in songbirds. Proc R Soc. B Biol Sci. 281:20140103.

Maher CR, Lott DF. 2000. A review of ecological determinants of territoriality within vertebrate species. Am Midl Nat. 143:1–29.

Mikula P, Tószögyová A, Hořák D, Petrusková T, Storch D, Albrecht T. 2019. Female solo song and duetting are associated with different territoriality in songbirds. Dryad Digital Repository. https://doi.org/10.5061/dryad.fn2z34tpr

Morton ES. 1996. A comparison of vocal behavior among tropical and temperate passerine birds. In: Kroodsma DE, Miller EH, editors. Ecology and evolution of acoustic communication in birds. New York, U.S.A.: Cornell Univ. Press. p. 258–268.

Najar N, Benedict L. 2015. Female song in New World wood warblers. Front Ecol Evol. 3:139.

Odom KJ, Hall ML, Riebel K, Omland KE, Langmore NE. 2014. Female song is widespread and ancestral in songbirds. Nat Commun. 5:3379.

Odom KJ, Omland KE, Price JJ. 2015. Differentiating the evolution of female song and male-female duets in the New World blackbirds: can tropical natural history traits explain duet evolution? Evolution. 69:839–847.

Paruelo JM, Epstein HE, Lauenroth WK, Burke IC. 1997. ANPP estimates from NDVI for the central grassland region of the United States. Ecology. 78:953–958.

Price JJ. 2009. Evolution and behavioral life-history correlates of female song in the New World blackbirds. Behav Ecol. 20:967–977.

Price JJ. 2015. Rethinking our assumptions about the evolution of bird song and other sexually dimorphic signals. Fron Ecol Evol. 3, 40.

Price JJ, Lanyon SM, Omland KE. 2009. Losses of female song with changes from tropical to temperate breeding in the New World blackbirds. Proc R Soc B Biol Sci. 276:1971–1980.

R Development Core Team. 2013. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing.

Ricklefs RE. 1969. The nesting cycle of songbirds in tropical and temperate regions. Living Bird. 8:165–175.

Robinson A. 1948. The biological significance of bird song in Australia. Emu. 48:291–315.

Schmidt H, Karnieli A. 2002. Analysis of the temporal and spatial vegetation patterns in a semi-arid environment observed by NOAA AVHRR imagery and spectral ground measurements. Int J Remote Sens. 23:3971–3990.

Seddon N, Tobias JA. 2003. Communal singing in the cooperatively breeding subdesert mesite *Monias benschi*: evidence of numerical assessment? J Avian Biol. 34:72–80.

Slater PJ, Mann NI. 2004. Why do the females of many bird species sing in the tropics?. J Avian Biol. 35:289–294.

Tobias JA, Sheard C, Seddon N, Meade A, Cotton AJ, Nakagawa S. 2016. Territoriality, social bonds, and the evolution of communal signaling in birds. Front Ecol Evol. 4:74.

Webb WH, Brunton DH, Aguirre D, Thomas D, Valcu M, Dale J. 2016. Female song occurs in songbirds with more elaborate female coloration and reduced sexual dichromatism. Front Ecol Evol. 4:22.

Figure 1. Associations between female song categories (duetting, female solo song, no duetting and no female song) and the level of (a) territoriality (weak, seasonal, year-round) and (b) social bonds (solitary, short-term, long-term). Each barplot represents different female song category and the height of differently colored bars within each category refers to the proportion of species associated with different levels of territoriality and social bonds. The number N represents the number of species in each group.

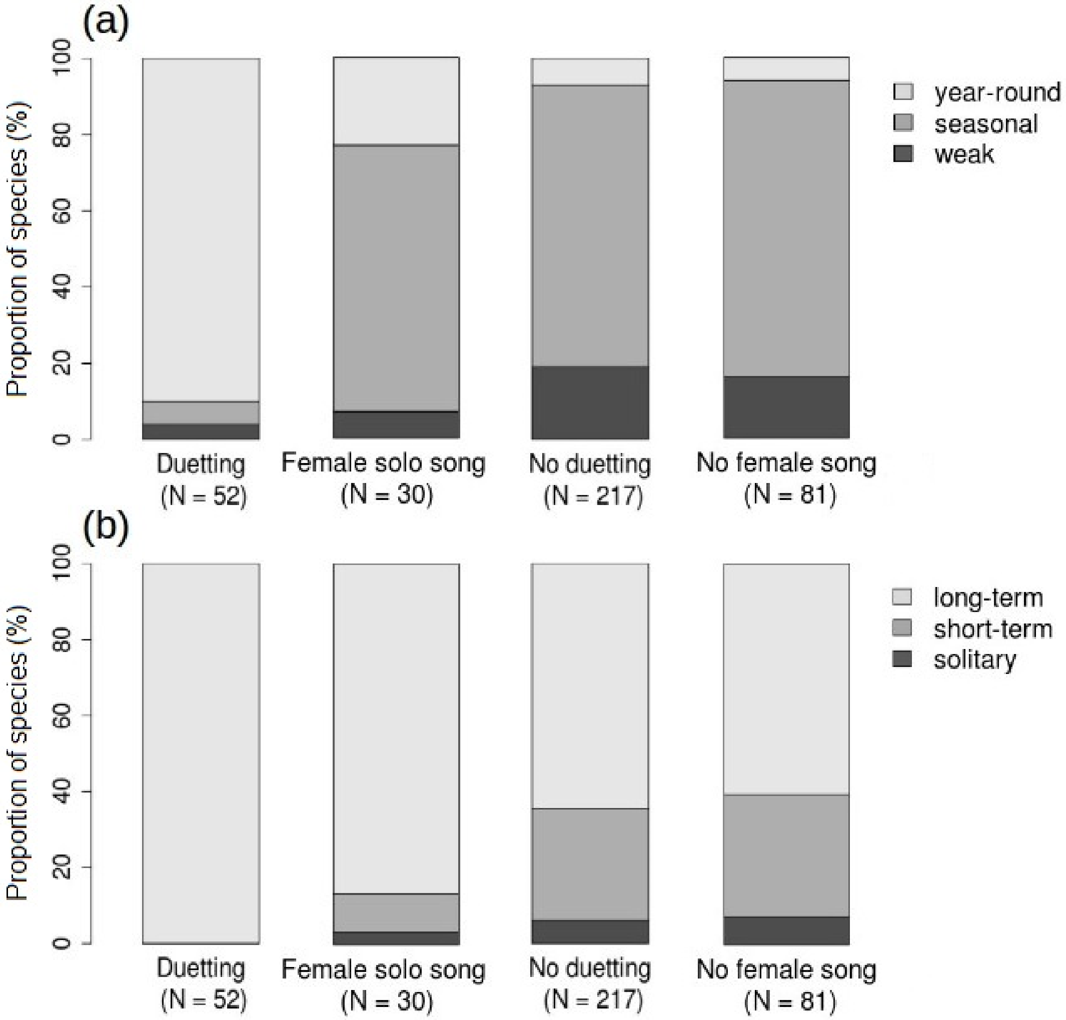


Figure 2. Geographical patterns in the proportion of species having (a) duets vs. no duets (N = 269 species), (b) duets vs. no female song (N = 133 species), (c) female solo song vs. duetting (N = 82 species), (d) female solo song vs. no female song (N = 111 species).

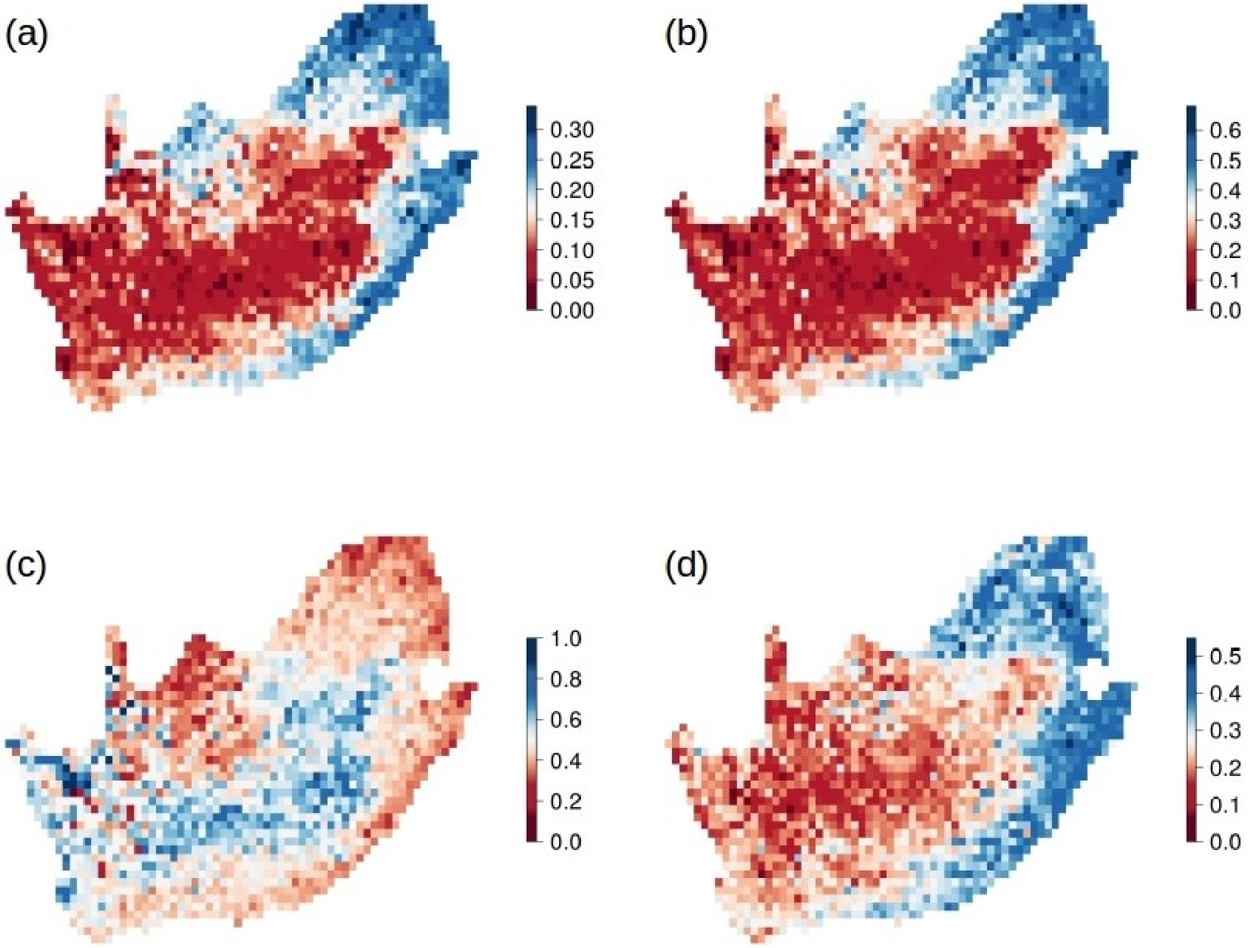


Table 1. Results of multivariable models based on a Markov chain Monte Carlo technique for generalized linear mixed-effect models with species-level phylogeny (the maximum credibility phylogenetic tree) as a random effect for (a) duetting (vs. no duetting, i.e. no female song and female solo song) (N = 269 species), (b) duetting (vs. no female song) (N = 133 species), (c) female solo song (vs. duetting) (N = 82 species), (d) female solo song (vs. no female song) (N = 111 species) as a response variables and life-history traits (territoriality, social bonds and cooperative breeding) and an environmental variable (NDVImax) as explanatory variables in songbirds of the South Africa and Lesotho. Estimates of the posterior mean with 95% credible intervals (lower and upper CI), posterior mode of the phylogenetic signal (lambda) and pMCMC values are reported. Statistically significant results are highlighted by bold.

Predictor	Posterior mean	95% CI	lambda	pMCMC
(a)				
Territoriality	455.42	231.16–701.29	0.645	<**0.001**
Social bonds*	–	–		–
Cooperative breeding	31.09	-111.77–173.11		0.653
NDVI$_{max}$	120.66	-154.84–402.10		0.376
(b)				
Territoriality	412.89	203.70–625.62	0.815	<**0.001**
Social bonds*	–	–	–	–
Cooperative breeding	58.35	-102.72–211.62		0.458
NDVI$_{max}$	225.80	-45.11–506.46		0.087
(c)				
Territoriality	-273.22	-517.45–-56.75	0.997	**0.006**
Social bonds	-59.93	-211.85–109.18		0.439
Cooperative breeding	-28.33	-266.44–204.10		0.821
NDVI$_{max}$	-42.06	-427.07–398.03		0.823
(d)				
Territoriality	186.50	-63.04–435.89	0.755	0.110
Social bonds	126.81	-131.47–405.33		0.321
Cooperative breeding	84.92	-236.30–390.08		0.550
NDVI$_{max}$	310.73	-186.44–881.82		0.212

Supplementary Material

Supplementary data are available at Behavioral Ecology online.

Table S1. Results of univariable models based on a Markov chain Monte Carlo technique for generalized linear mixed-effect models with species-level phylogeny (the maximum credibility phylogenetic tree) as a random effect for (a) duetting (vs. no duetting, i.e. no female song and female solo song) (N = 269 species), (b) duetting (vs. no female song) (N = 133 species), (c) female solo song (vs. duetting) (N = 82 species), (d) female solo song (vs. no female song) (N = 111 species) as a response variables and life-history traits (territoriality, social bonds and cooperative breeding) and an environmental variable ($NDVI_{max}$) as explanatory variables in songbirds of the South Africa and Lesotho. Estimates of the posterior mean with 95% credible intervals (lower and upper CI), posterior mode of the phylogenetic signal (lambda) and pMCMC values are reported. Statistically significant results are highlighted by bold.

Table S2. Results of multivariable and univariable models based on a Markov chain Monte Carlo technique for generalized linear mixed-effect models with species-level phylogeny (100 randomly selected phylogenetic trees, their combined output is reported) as a random effect for (a) duetting (vs. no duetting, i.e. no female song and female solo song) (N = 269 species), (b) duetting (vs. no female song) (N = 133 species), (c) female solo song (vs. duetting) (N = 82 species), (d) female solo song (vs. no female song) (N = 111 species) as a response variables and life-history traits (territoriality, social bonds and cooperative breeding) and an environmental variable ($NDVI_{max}$) as explanatory variables in songbirds of the South Africa and Lesotho. Estimates of the posterior mean with 95% credible intervals (lower and upper CI), posterior mode of the phylogenetic signal (lambda) and pMCMC values are reported. Statistically significant results are highlighted by bold.

Table S3. Results of multivariable and univariable models based on a Markov chain Monte Carlo technique for generalized linear mixed-effect models with family-level phylogeny (the maximum credibility phylogenetic tree) as a random effect for (a) duetting (vs. no duetting, i.e. no female song and female solo song) (N = 269 species), (b) duetting (vs. no female song) (N = 133 species), (c) female solo song (vs. duetting) (N = 82 species), (d) female solo song (vs. no female song) (N = 111 species) as a response variables and life-history traits (territoriality, social bonds and cooperative breeding) and an environmental variable (NDVImax) as explanatory variables in songbirds of the South Africa and Lesotho. Estimates of the posterior mean with 95% credible intervals (lower and upper CI), posterior mode of the phylogenetic signal (lambda) and pMCMC values are reported. Statistically significant results are highlighted by bold.

Table S4. Results of multivariable and univariable models based on a Markov chain Monte Carlo technique for generalized linear mixed-effect models with family-level phylogeny (100 randomly selected phylogenetic trees, their combined output is reported) as a random effect for (a) duetting (vs. no duetting, i.e. no female song and female solo song) (N = 269 species), (b) duetting (vs. no female song) (N = 133 species), (c) female solo song (vs. duetting) (N = 82 species), (d) female solo song (vs. no female song) (N = 111 species) as a response variables and life-history traits (territoriality, social bonds and cooperative breeding) and an environmental variable ($NDVI_{max}$) as explanatory variables in songbirds of the South Africa and Lesotho. Estimates of the posterior mean with 95% credible intervals (lower and upper CI), posterior mode of the phylogenetic signal (lambda) and pMCMC values are reported. Statistically significant results are highlighted by bold.

Table S5. The autocorrelation values among stored samples (Lag 5000) from the posterior of multivariable and univariable models based on a Markov chain Monte Carlo technique for generalized linear mixed-effect models with family-level phylogeny (the maximum credibility phylogenetic tree) as a random effect. The level of the independence of the samples in the posterior was very high, which means that the iteration chains mixed well. The values of autocorrelation refer to the following models: (a) duetting vs. no duetting (i.e. no female song and female solo song), (b) duetting vs. no female song, (c) female solo song vs. duetting, (d) female solo song vs. no female song.

Table S6. Results of univariable models based on a Markov chain Monte Carlo technique for generalized linear mixed-effect models with species-level phylogeny (the maximum credibility phylogenetic tree) as a random effect for (a) duetting (vs. no duetting, i.e. no female song and female solo song) (N = 269 species), (b) duetting (vs. no female song) (N = 133 species), (c) female solo song (vs. duetting) (N = 82 species), (d) female solo song (vs. no female song) (N = 111 species) as a response variables and life-history traits (territoriality, social bonds and cooperative breeding) and an environmental variable ($NDVI_{max}$) as explanatory variables in songbirds of the South Africa and Lesotho. In contrast to model results reported in Table 1 and Table S1–S5 where territoriality, social bonds and cooperative breeding were treated as continuous variables, here, these variables were coded as categorical predictors. Estimates of the posterior mean with 95% credible intervals (lower and upper CI), posterior mode of the phylogenetic signal (lambda) and pMCMC values are reported. Statistically significant results are highlighted by bold.

Table S7. Results of multivariable and univariable models based on a Markov chain Monte Carlo technique for generalized linear mixed-effect models with family-level phylogeny (the maximum credibility phylogenetic tree) as a random effect for (a) duetting (vs. no duetting, i.e. no female song and female solo song) (N = 269 species), (b) duetting (vs. no female song) (N = 133 species), (c) female solo song (vs. duetting) (N = 82 species), (d) female solo song (vs. no female song) (N = 111 species) as a response variables and life-history traits (territoriality, social bonds and cooperative breeding) and an environmental variable ($NDVI_{max}$) as explanatory variables in songbirds of the South Africa and Lesotho. In contrast to model results reported in Table 1 and Table S1–S5 where territoriality, social bonds and cooperative breeding were treated as continuous variables, here, these variables were coded as categorical predictors. Estimates of the posterior mean with 95% credible intervals (lower and upper CI), posterior mode of the phylogenetic signal (lambda) and pMCMC values are reported. Statistically significant results are highlighted by bold.

Figure S1. Geographical patterns in the proportion of particular territoriality type: (a) year-round territoriality, (b) seasonal territoriality, (c) no territoriality; and environmental conditions: (d) $NDVI_{max}$ across local assemblages (0.25° × 0.25° grid cell) of South African songbirds (N = 163 species).

Table S1. Results of univariable models based on a Markov chain Monte Carlo technique for generalized linear mixed-effect models with species-level phylogeny (the maximum credibility phylogenetic tree) as a random effect for (a) duetting (vs. no duetting, i.e. no female song and female solo song) (N = 269 species), (b) duetting (vs. no female song) (N = 133 species), (c) female solo song (vs. duetting) (N = 82 species), (d) female solo song (vs. no female song) (N = 111 species) as a response variables and life-history traits (territoriality, social bonds and cooperative breeding) and an environmental variable (NDVI_{max}) as explanatory variables in songbirds of the South Africa and Lesotho. Estimates of the posterior mean with 95% credible intervals (lower and upper CI), posterior mode of the phylogenetic signal (lambda) and pMCMC values are reported. Statistically significant results are highlighted by bold.

Predictor	**Posterior mean**	**95% CI**	**lambda**	**pMCMC**
(a)				
Territoriality	402.20	158.82–629.07	0.758	**<0.0001**
Social bonds*	–	–	–	–
Cooperative breeding	55.94	-49.79–169.80	0.923	0.274
NDVI_{max}	134.80	-62.80–348.86	0.998	0.163
(b)				
Territoriality	376.73	157.43–589.84	0.960	**<0.0001**
Social bonds*	–	–	–	–
Cooperative breeding	72.56	-55.10–210.89	0.874	0.248
NDVI_{max}	205.04	-10.19–456.26	0.996	0.052
(c)				
Territoriality	-277.74	-511.67—67.84	0.908	**0.001**
Social bonds	-112.00	-262.40–38.40	0.994	0.139
Cooperative breeding	-52.09	-287.19–166.76	0.953	0.622
NDVI_{max}	-40.77	-423.25–317.69	0.999	0.803
(d)				
Territoriality	223.27	27.98–437.88	0.705	**0.014**
Social bonds	195.89	-5.25–464.46	0.724	0.054
Cooperative breeding	76.82	-215.08–379.71	0.727	0.572
NDVI_{max}	377.74	-74.13–940.43	0.653	0.097

*Because all species singing in duets belonged to one social-bond (long-term) category, it was not possible to establish social bonds as an explanatory variable

Table S2. Results of multivariable and univariable models based on a Markov chain Monte Carlo technique for generalized linear mixed-effect models with species-level phylogeny (100 randomly selected phylogenetic trees, their combined output is reported) as a random effect for (a) duetting (vs. no duetting, i.e. no female song and female solo song) (N = 269 species), (b) duetting (vs. no female song) (N = 133 species), (c) female solo song (vs. duetting) (N = 82 species), (d) female solo song (vs. no female song) (N = 111 species) as a response variables and life-history traits (territoriality, social bonds and cooperative breeding) and an environmental variable (NDVI_{max}) as explanatory variables in songbirds of the South Africa and Lesotho. Estimates of the posterior mean with 95% credible intervals (lower and upper CI), posterior mode of the phylogenetic signal (lambda) and pMCMC values are reported. Statistically significant results are highlighted by bold.

Predictor	**Posterior mean**		**95% CI**		**lambda**		**pMCMC**	
	Multivariable	**Univariable**	**Multivariable**	**Univariable**	**Multivariable**	**Univariable**	**Multivariable**	**Univariable**
(a)								
Territoriality	458.23	291.86	226.26–703.37	81.46–490.81	0.632	0.715	**<0.0001**	**<0.0001**
Social bonds*	–	–	–	–		–	–	–
Cooperative breeding	28.83	40.39	-112.10–172.36	-56.71–148.51		0.899	0.673	0.396
NDVI_{max}	125.87	114.70	-143.26–410.58	-56.98–315.19		0.963	0.353	0.170
(b)								
Territoriality	410.65	374.25	207.88–619.87	156.89–590.14	0.977	0.878	**<0.0001**	**<0.0001**
Social bonds*	–	–	–	–		–	–	–
Cooperative breeding	56.57	65.12	-100.25–214.44	-63.53–205.52		0.945	0.464	0.312
NDVI_{max}	226.83	197.90	-37.67–509.71	-19.60–443.86		0.975	0.085	0.062

(c)								
Territoriality	-270.83	-275.74	-509.34–-51.98	-502.53–-63.85	0.987	0.796	**0.006**	**0.002**
Social bonds	-60.19	-111.43	-217.29–101.76	-260.12–37.77		0.933	0.443	0.141
Cooperative breeding	-31.20	-52.05	-270.60–198.06	-281.49–166.54		0.937	0.787	0.629
NDVI$_{max}$	-37.44	-47.42	-451.20–377.33	-447.29–344.14		0.946	0.827	0.799
(d)								
Territoriality	188.06	221.40	-46.24–440.05	29.51–432.89	0.786	0.754	0.104	**0.012**
Social bonds	123.18	198.24	-130.56–401.81	-20.18–450.40		0.667	0.335	0.055
Cooperative breeding	89.73	78.36	-220.76–402.16	-207.90–372.86		0.702	0.535	0.558
NDVI$_{max}$	300.60	367.48	-205.54–856.41	-95.32–905.34		0.695	0.224	0.104

*Because all species singing in duets belonged to one social-bond (long-term) category, it was not possible to establish social bonds as an explanatory variable

Tables S3-S5. Every species in our dataset was represented by a single sample within which variation was not considered. A potential consequence of this approach is that the random effect of the species could potentially be confounded with the residuals (Hadfield 2010). To avoid this obstacle and test the robustness of these results, we also performed the same models with different parameterization using family-level phylogeny. We used an inverse-gamma prior for random effects and an uninformative prior for residual variance in all MCMCglmms. The choice of priors was determined by the character of our data, sometimes containing a small number of samples for some variable categories. All models were run for 5,000,000 iterations with elimination of the first 20,000 iterations as a burn-in period and thinning to every 5000th iteration. For models with a maximum credibility phylogenetic tree, we used the Gelman-Rubin statistic to check for convergence of multiple MCMC chains runs in parallel. The iteration chains mixed well, exhibiting no observable autocorrelation. The Gelman-Rubin statistic threshold was established to 1.09 in all models.

References

Hadfield JD. 2010. MCMCglmm course notes. Available at http://cran.r-project.org/web/packages/MCMCglmm/vignettes/CourseNotes.pdf

Table S3. Results of multivariable and univariable models based on a Markov chain Monte Carlo technique for generalized linear mixed-effect models with family-level phylogeny (the maximum credibility phylogenetic tree) as a random effect for (a) duetting (vs. no duetting, i.e. no female song and female solo song) (N = 269 species), (b) duetting (vs. no female song) (N = 133 species), (c) female solo song (vs. duetting) (N = 82 species), (d) female solo song (vs. no female song) (N = 111 species) as a response variables and life-history traits (territoriality, social bonds and cooperative breeding) and an environmental variable (NDVI_{max}) as explanatory variables in songbirds of the South Africa and Lesotho. Estimates of the posterior mean with 95% credible intervals (lower and upper CI), posterior mode of the phylogenetic signal (lambda) and pMCMC values are reported. Statistically significant results are highlighted by bold.

Predictor	**Posterior mean**		**95% CI**		**lambda**		**pMCMC**	
	Multivariable	**Univariable**	**Multivariable**	**Univariable**	**Multivariable**	**Univariable**	**Multivariable**	**Univariable**
(a)								
Territoriality	463.38	408.14	238.33–729.25	137.11–667.40	0.360	0.589	**<0.001**	**<0.001**
Social bonds*	–	–	–	–		–	–	–
Cooperative breeding	14.47	34.94	-117.85–156.52	-55.17–140.45		0.801	0.833	0.454
NDVI_{max}	110.13	100.40	-144.32–387.75	-67.86–298.04		0.832	0.396	0.217
(b)								
Territoriality	412.47	363.87	230.18–650.76	118.46–588.66	0.570	0.710	**<0.001**	**<0.001**
Social bonds*	–	–	–	–	–	–	–	–
Cooperative breeding	48.64	71.45	-101.60–205.34	-33.16–212.95		0.769	0.496	0.169
NDVI_{max}	185.68	136.17	-45.45–462.91	-50.49–367.89		0.896	0.114	0.116

(c)								
Territoriality	-314.39	-282.32	-563.23–-102.21	-510.77–-83.53	0.671	0.765	**<0.001**	**<0.001**
Social bonds	-61.48	-116.96	-236.47–101.23	-257.39–33.31		0.823	0.488	0.122
Cooperative breeding	-4.62	-12.90	-250.54–206.77	-207.40–180.00		0.826	0.980	0.898
NDVI$_{max}$	-18.70	-64.42	-511.52–366.85	-478.10–249.50		0.845	0.918	0.671
(d)								
Territoriality	237.13	237.17	7.60–507.24	34.21–465.40	0.762	0.742	0.060	**0.008**
Social bonds	114.25	185.70	-127.98–447.22	-37.02–430.91		0.479	0.416	0.086
Cooperative breeding	170.98	135.89	-139.99–477.11	-137.48–405.90		0.607	0.219	0.267
NDVI$_{max}$	210.48	272.18	-259.87–775.81	-147.38–776.89		0.527	0.446	0.233

*Because all species singing in duets belonged to one social-bond (long-term) category, it was not possible to establish social bonds as an explanatory variable

Table S4. Results of multivariable and univariable models based on a Markov chain Monte Carlo technique for generalized linear mixed-effect models with family-level phylogeny (100 randomly selected phylogenetic trees, their combined output is reported) as a random effect for (a) duetting (vs. no duetting, i.e. no female song and female solo song) (N = 269 species), (b) duetting (vs. no female song) (N = 133 species), (c) female solo song (vs. duetting) (N = 82 species), (d) female solo song (vs. no female song) (N = 111 species) as a response variables and life-history traits (territoriality, social bonds and cooperative breeding) and an environmental variable ($NDVI_{max}$) as explanatory variables in songbirds of the South Africa and Lesotho. Estimates of the posterior mean with 95% credible intervals (lower and upper CI), posterior mode of the phylogenetic signal (lambda) and pMCMC values are reported. Statistically significant results are highlighted by bold.

Predictor	**Posterior mean**		**95% CI**		**lambda**		**pMCMC**	
	Multivariable	**Univariable**	**Multivariable**	**Univariable**	**Multivariable**	**Univariable**	**Multivariable**	**Univariable**
(a)								
Territoriality	448.48	308.93	211.35–685.02	96.45–515.31	0.467	0.555	**<0.001**	**<0.001**
Social bonds*	–	–	–	–		–	–	–
Cooperative breeding	12.58	35.90	-119.44–146.57	-54.23–138.02		0.841	0.837	0.419
$NDVI_{max}$	113.38	99.16	-132.39–377.81	-65.14–296.38		0.843	0.368	0.221
(b)								
Territoriality	411.00	358.71	199.02–622.64	119.76–587.41	0.397	0.701	**<0.001**	**<0.001**
Social bonds*	–	–	–	–		–	–	–
Cooperative breeding	48.25	70.70	-95.71–197.02	-36.84–196.87		0.820	0.500	0.179
$NDVI_{max}$	189.20	133.84	-55.22–456.34	-47.86–352.20		0.837	0.118	0.129

(c)								
Territoriality	-314.50	-278.92	-556.02–-89.87	-503.43–-62.32	0.706	0.701	**0.002**	**<0.001**
Social bonds	-60.85	-116.15	-229.96–109.36	-269.15–32.94		0.850	0.476	0.131
Cooperative breeding	-5.49	-7.36	-235.85–221.95	-205.32–183.05		0.853	0.968	0.949
NDVI_{max}	-20.65	-67.94	-427.01–389.75	-414.72–253.03		0.850	0.827	0.656
(d)								
Territoriality	231.73	231.69	-16.98–496.42	28.70–452.63	0.706	0.758	0.062	**0.010**
Social bonds	113.71	181.72	-150.49–403.11	-30.73–439.26		0.601	0.404	0.074
Cooperative breeding	173.23	139.81	-125.23–477.43	-115.86–417.28		0.623	0.240	0.257
NDVI_{max}	194.76	275.07	-325.32–751.95	-166.64–787.60		0.596	0.453	0.206

*Because all species singing in duets belonged to one social-bond (long-term) category, it was not possible to establish social bonds as an explanatory variable

Table S5. The autocorrelation values among stored samples (Lag 5000) from the posterior of multivariable and univariable models based on a Markov chain Monte Carlo technique for generalized linear mixed-effect models with family-level phylogeny (the maximum credibility phylogenetic tree) as a random effect. The level of the independence of the samples in the posterior was very high, which means that the iteration chains mixed well. The values of autocorrelation refer to the following models: (a) duetting vs. no duetting (i.e. no female song and female solo song), (b) duetting vs. no female song, (c) female solo song vs. duetting, (d) female solo song vs. no female song.

Model	**Territoriality**	**Social bonds**	**Cooperative breeding**	**NDVI_{max}**	**Family**	**Units**
Multivariable						
(a)	-0.0051	–	-0.0062	0.0151	-0.0434	-0.0381
(b)	-0.0252	–	0.0473	-0.0029	0.0068	-0.0407
(c)	-0.0565	-0.0235	-0.0160	0.0308	-0.0046	-0.0103
(d)	0.0119	-0.0030	-0.0501	-0.0053	0.0975	0.0071
Univariable						
(a)	-0.0244	–	–	–	0.0579	-0.0367
(a)	–	–	0.0231	–	0.0208	0.0392
(a)	–	–	–	-0.0226	0.0204	-0.0355
(b)	-0.0007	–	–	–	-0.0054	0.0271
(b)	–	–	-0.0004	–	0.0439	0.0281
(b)	–	–	–	0.0455	-0.0406	0.0596
(c)	-0.0262	–	–	–	-0.0007	-0.0035
(c)	–	-0.0588	–	–	-0.0299	-0.0331
(c)	–	–	-0.0006	–	0.0094	-0.0001
(c)	–	–	–	-0.0164	0.0067	0.0054
(d)	-0.0561	–	–	–	-0.0056	-0.0323
(d)	–	0.0266	–	–	-0.0118	0.0476
(d)	–	–	0.0027	–	0.0552	-0.0421
(d)	–	–	–	0.0142	0.0027	0.0039

Tables S6-S7. In addition to models where territoriality, social bonds and cooperative were coded as continuous variables, we prepared a set of models where these variables were coded as categorical variables. We performed these models using both species- and family level phylogeny. We used an inverse-gamma prior for random effects and an uninformative prior for residual variance in all MCMCglmms. The choice of priors was determined by the character of our data, sometimes containing a small number of samples for some variable categories. All models were run for 5,000,000 iterations with elimination of the first 20,000 iterations as a burn-in period and thinning to every 5000th iteration. We used a maximum credibility phylogenetic tree and the Gelman-Rubin statistic to check for convergence of multiple MCMC chains runs in parallel. The iteration chains mixed well, exhibiting no observable autocorrelation. The Gelman-Rubin statistic threshold was established to 1.09 in all models.

Table S6. Results of multivariable and univariable models based on a Markov chain Monte Carlo technique for generalized linear mixed-effect models with species-level phylogeny (the maximum credibility phylogenetic tree) as a random effect for (a) duetting (vs. no duetting, i.e. no female song and female solo song) (N = 269 species), (b) duetting (vs. no female song) (N = 133 species), (c) female solo song (vs. duetting) (N = 82 species), (d) female solo song (vs. no female song) (N = 111 species) as a response variables and life-history traits (territoriality, social bonds and cooperative breeding) and an environmental variable ($NDVI_{max}$) as explanatory variables in songbirds of the South Africa and Lesotho. In contrast to model results reported in Table 1 and Table S1–S5 where territoriality, social bonds and cooperative breeding were treated as continuous variables, here, these variables were coded as categorical predictors. Estimates of the posterior mean with 95% credible intervals (lower and upper CI), posterior mode of the phylogenetic signal (lambda) and pMCMC values are reported. Statistically significant results are highlighted by bold.

Predictor	**Posterior mean**		**95% CI**		**lambda**		**pMCMC**	
	Multivariable	**Univariable**	**Multivariable**	**Univariable**	**Multivariable**	**Univariable**	**Multivariable**	**Univariable**
(a)								
Territoriality (seasonal)	-543.94	-495.72	-829.61–-266.11	-750.70–-222.68	0.478	0.520	**<0.001**	**<0.001**
Territoriality (weak)	-484.12	-442.66	-778.30–-216.51	-701.41–-168.25			**<0.001**	**<0.001**
Social bonds*	–	–	–	–		–	–	–
Cooperative breeding	23.27	47.42	-122.91–158.28	-42.51–152.87		0.873	0.743	0.308
$NDVI_{max}$	108.76	134.80	-151.79–423.57	-62.80–348.86		0.998	0.390	0.163
(b)								
Territoriality (seasonal)	-503.85	-459.35	-709.04–-258.84	-706.13–-220.39	0.427	0.667	**<0.001**	**<0.001**
Territoriality (weak)	-433.40	-414.69	-662.13–-199.02	-688.84–-196.43			**<0.001**	**<0.001**
Social bonds*	–	–	–	–	–	–	–	–
Cooperative breeding	44.12	60.69	-126.83–199.02	-53.34–191.26		0.877	0.567	0.290
$NDVI_{max}$	249.50	205.04	-48.04–510.83	-10.19–456.26		0.996	0.078	0.052

(c)								
Territoriality (seasonal)	473.97	418.56	187.33–754.17	174.04–683.88	0.757	0.732	**0.002**	**<0.001**
Territoriality (weak)	123.12	231.42	-257.74–559.20	-56.02–568.40			0.543	0.129
Social bonds (short)	-414.51	-115.30	-1242.35–396.92	-831.40–554.80		0.867	0.327	0.769
Social bonds (long)	-555.22	-349.80	-1288.72–172.76	-938.40–183.80			0.118	0.257
Cooperative breeding	15.05	-38.06	-200.68–243.80	-242.16–149.41		0.873	0.851	0.673
NDVI$_{max}$	124.89	-40.77	-358.91–590.10	-423.25–317.69		0.999	0.569	0.803
(d)								
Territoriality (seasonal)	-166.05	-208.83	-510.35–147.59	-505.01–48.61	0.686	0.728	0.290	0.118
Territoriality (weak)	-590.36	-618.66	-1270.55–83.49	-1259.45–-85.99			0.065	**0.010**
Social bonds (short)	-276.37	208.84	-1104.90–507.99	-335.52–945.22		0.658	0.443	0.500
Social bonds (long)	-85.52	381.09	-873.69–625.25	-140.52–1033.26			0.814	0.141
Cooperative breeding	106.84	147.12	-262.64–455.41	-130.23–419.45		0.689	0.518	0.259
NDVI$_{max}$	306.75	377.74	-262.49–915.19	-74.13–940.43		0.653	0.292	0.097

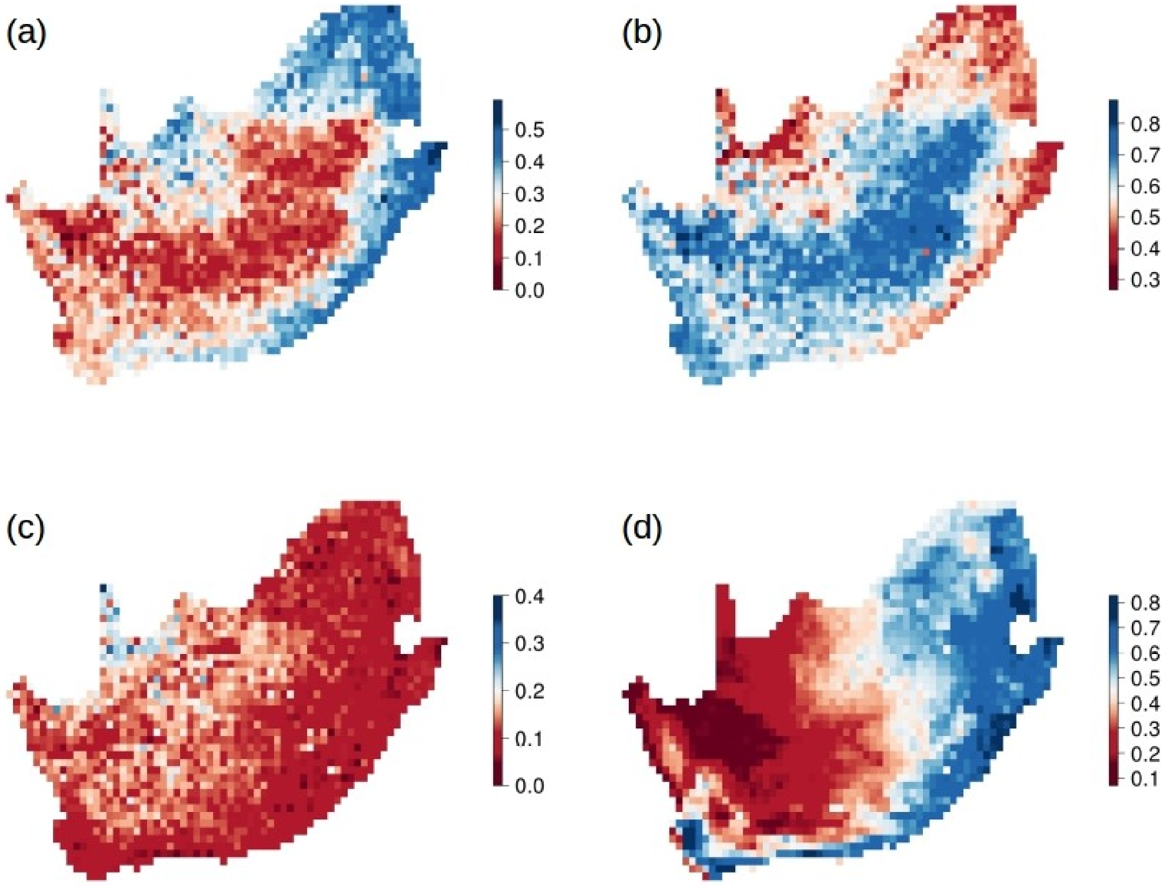
Table S7. Results of multivariable and univariable models based on a Markov chain Monte Carlo technique for generalized linear mixed-effect models with family-level phylogeny (the maximum credibility phylogenetic tree) as a random effect for (a) duetting (vs. no duetting, i.e. no female song and female solo song) (N = 269 species), (b) duetting (vs. no female song) (N = 133 species), (c) female solo song (vs. duetting) (N = 82 species), (d) female solo song (vs. no female song) (N = 111 species) as a response variables and life-history traits (territoriality, social bonds and cooperative breeding) and an environmental variable (NDVI_{max}) as explanatory variables in songbirds of the South Africa and Lesotho. In contrast to model results reported in Table 1 and Table S1–S5 where territoriality, social bonds and cooperative breeding were treated as continuous variables, here, these variables were coded as categorical predictors. Estimates of the posterior mean with 95% credible intervals (lower and upper CI), posterior mode of the phylogenetic signal (lambda) and pMCMC values are reported. Statistically significant results are highlighted by bold.

Predictor	**Posterior mean**		**95% CI**		**lambda**		**pMCMC**	
	Multivariable	**Univariable**	**Multivariable**	**Univariable**	**Multivariable**	**Univariable**	**Multivariable**	**Univariable**
(a)								
Territoriality (seasonal)	-605.91	-544.80	-886.33–-308.21	-855.18–-263.23	0.555	0.595	**<0.001**	**<0.001**
Territoriality (weak)	-530.94	-476.81	-812.50–-262.51	-758.20–-196.01			**<0.001**	**<0.001**
Social bonds*	–	–	–	–		–	–	–
Cooperative breeding	-3.58	34.73	-159.54–150.52	-54.01–139.34		0.796	0.956	0.422
NDVI_{max}	89.24	100.40	-183.35–354.43	-67.86–298.04		0.832	0.532	0.217
(b)								
Territoriality (seasonal)	-520.81	-483.23	-775.70–-296.78	-766.18–-230.24	0.471	0.621	**<0.001**	**<0.001**
Territoriality (weak)	-448.59	-431.60	-698.67–-221.69	-684.87–-179.20			**<0.001**	**<0.001**
Social bonds*	–	–	–	–	–	–	–	–
Cooperative breeding	31.83	66.67	-134.34–190.09	-46.27–192.70		0.762	0.675	0.211
NDVI_{max}	217.53	136.17	-44.55–480.98	-50.49–367.89		0.896	0.110	0.116

(c)								
Territoriality (seasonal)	487.79	425.73	241.67–744.20	175.46–669.43	0.660	0.644	**<0.001**	**<0.001**
Territoriality (weak)	163.27	256.19	-352.42–605.40	-32.28–583.88			0.402	0.100
Social bonds (short)	-411.74	-250.10	-1458.01–403.11	-1271.20–545.80		0.775	0.394	0.631
Social bonds (long)	-537.66	-448.40	-1318.37–362.18	-1309.70–331.10			0.177	0.261
Cooperative breeding	22.28	-8.88	-187.25–209.85	-203.81–181.99		0.773	0.777	0.918
$NDVI_{max}$	159.67	-64.42	-224.39–573.48	-478.10–249.50		0.845	0.420	0.671
(d)								
Territoriality (seasonal)	-204.35	-208.83	-537.77–121.21	-505.01–48.61	0.686	0.721	0.189	0.118
Territoriality (weak)	-770.66	-618.66	-1689.02–-42.04	-1259.45–-85.99			**0.032**	**0.010**
Social bonds (short)	-192.49	208.84	-1205.64–976.49	-335.52–945.22		0.584	0.681	0.500
Social bonds (long)	-66.17	381.09	-1128.72–999.23	-140.52–1033.26			0.908	0.141
Cooperative breeding	205.42	147.12	-168.16–501.09	-130.23–419.45		0.600	0.249	0.259
$NDVI_{max}$	172.18	272.18	-523.10–689.03	-147.38–776.89		0.527	0.568	0.233

*Because all species singing in duets belonged to one social-bond (long-term) category, it was not possible to establish social bonds as an explanatory variable

Figure S1. Geographical patterns in the proportion of particular territoriality type: (a) year-round territoriality, (b) seasonal territoriality, (c) no territoriality; and environmental conditions: (d) $\mathrm{NDVI}_{\mathrm{max}}$ across local assemblages (0.25° × 0.25° grid cell) of South African songbirds (N = 163 species).



Chapter 5

Productive environments host colourful birds: Geographical patterns in avian plumage colouration in South Africa

Anna Tószögyová[1,2], David Hořák[1], Tereza Kubíková, David Storch[1,2]

[1]*Department of Ecology, Faculty of Science, Charles University, Czech Republic, anna83@seznam.cz*

[2]*Center for Theoretical Study, Charles University and the Academy of Sciences of the Czech Republic, Czech Republic*

Abstract

The idea that birds in tropical areas have the most colourful plumage is long-standing, although recent studies do not consistently support the colourful tropics hypothesis. High colourfulness of tropical birds may be given by the availability and diversity of resources for dietary pigments and by the complexity of habitats which may influence colouration through the selection pressure on the development of cryptic and signalling functions. These aspects of the tropical environment are linked with high environmental productivity. Here, we hypothesize that bird colouration predictably varies with environmental productivity. We compiled data on 13 colour characteristics in all 579 South African breeding species with regard to pigment types, ornaments/ patterns and brightness/saturation, and analysed their spatial patterns in relation to the geographical gradient in environmental productivity. We found that more colourful species, species having carotenoids in feathers (yellow-orange-red), and green-blue or predominantly black and iridescent species occurr mainly in productive habitats such as humid savanna and woodlands in the north-east of South Africa. On the contrary, pale grey-brown or brighter species and species with black tips of tail and wings live in arid and unproductive habitats on the west. Resolving the colourful tropics hypothesis can help to reveal many inter- and intraspecific interactions; competition for mates or resources, sexual selection and camouflage from predators.

Key-words: bird feather colouration, colourfulness, conspicuousness, feather pigments, environmental productivity, South African birds

Introduction

Biologists have always been interested in differences among species and the causes of these differences across the world. The differences in morphological characteristics such as body size, shape or length of body extremities have been well studied in all animal taxa, often in relation to how species can cope with different environmental conditions. Thermoregulatory adaptations to decreasing temperature towards from the equator lead to the quite predictable geographical patterns in morphology (Bergmann, 1847; Allen, 1877). The colouration of animals is no less obvious feature, but its determination is more difficult and large-scale studies of variation in colouration are rare. Birds are an excellent group of species for studying considerable differences in colouration. The cause of various avian colouration lies in its different functional significance. Many functions of avian colouration such as signal role, crypsis, thermoregulation or mechanical and bacterial protection have been reported (Burtt, 1981, 1986; Butcher & Rohwer, 1989; Savalli, 1995) and they have been mostly discussed in the context of a direct conflict between natural and sexual selection (Baker & Parker, 1979; Endler, 1978, 1992). Different adaptive functions of colours are favoured in different environments (McNaught & Owens, 2002), resulting in high plumage colour variation among habitats. It is thus no wonder that the geographical patterns in bird colouration seem to be very complex.

The first observations lead to the widespread idea that tropical birds are the most colourful (Wilson & von Neumann, 1972), however, studies examining rigorously geographical patterns in avian colouration are rare (but see Dalrymple et al., 2015; Friedman & Remeš, 2017). Evidence documenting more colourful birds in tropics is incomplete mainly due to the focus on a single taxonomic group, a single colour trait or limited spatial perspective. There are a few exceptions. A pioneer study by Wilson and von Neumann (1972) concluded that tropical birds of South America are more frequently colourful than those from non-tropical regions or birds of North America and Europe. However, the authors used a very simple subjective categorization of colourfulness into two groups, i.e. colourful or not. Delhey, Smith, and Peters (2013) found that more colour-variable parrots and passerine birds of Australia occupy larger ranges and are less vulnerable to the threat of extinction. Nevertheless, they did not address the issue of spatial variation explicitly. The conclusions of some studies have, in contrast, disproved the hypothesis about more colourful biota in tropics. Bailey (1978) found no latitudinal gradient in colourfulness of passerine birds of North and Middle America. The author also strongly suspected the correctness of the methodology and the subsequent results of the Wilson and von Neumann’s (1972) study. Similarly, Dalrymple et al. (2015) demonstrated that birds (together with butterflies and flowers) of Australia display geographical patterns in colourfulness, but tropical birds are not more colourful than their temperate counterparts. Friedman and Remeš (2017) found that birds from two passerine families from tropical regions of Australia do not evolve more colourful feathers compared to their relatives from temperate regions. In general, birds with their plumage colours show apparent spatial patterns that are in a certain relation to environmental variables, but it has not been confirmed that tropical birds are more colourful.

Nevertheless, the colourful tropics hypothesis is significantly persistent. The question is, what could be a potential driver of greater plumage colouration in the tropics. The fact that a tropical environment appears to host more colourful birds can only be the result of higher species richness of this environment (Bailey, 1978; Dalrymple et al., 2015). Although the number of more colourful species is increasing towards tropical areas, their proportional representation may not vary to such an extent that it could be argued that tropical inhabitants are more vivid. The another factor responsible for greater colourfulness of tropical birds can be the higher availability and diversity of tropical food resources. The increase in different dietary preferences in more productive tropical environments suggests that there is a positive relationship between productivity and vegetation complexity which provides greater heterogeneity in food availability (Karr & Brawn, 1990; Bailey et al., 2004). The habitats with high and diverse plant productivity offer birds a wide range of food resources such as insects, fruits, nectar, buds (Bailey et al., 2004). And it is known that the production of some feather pigments is dependent on the acquisition of resources. For instance, the development of carotenoid pigmentation, yellow-orange-red colouration, is strongly influenced by the sufficient nutritional value of food, as carotenoid-based pigments cannot be synthesized but only ingested (McGraw, 2006). The production of melanin-based and structural colours is also affected by diet (Hill, 2006). Therefore, food availability and its diversity allow birds to develop colourful and striking plumage. The other assumption supporting the colourful tropics hypothesis may be based on the overall diversity of tropical environments, where sexually selected traits can be applied to a greater extent than in less productive environments (Owens, Bennett, & Harvey, 1999; Dale, Dey, Delhey, Kempenaers, & Valcu, 2015). The complex vegetation structure of tropical habitats represents a suitable environment where sexual signals can be expressed in the form of colour displays. There are several possible reasons for that. Dense vegetation allows release the selection pressure on cryptic colouration as species can be more easily hidden from predators (Gomez & Théry, 2007). Therefore, due to lower visibility over longer distances in tropical environments, there is an opportunity for more intense visual expression of quality as mates or territorial competitors, as the visual recipients of these signals can be less distant than predators. Strong sexual selection on males would not only lead to their greater colourfulness but also to greater dichromatism between the sexes (Dale et al., 2015). Nevertheless, the geographical distribution of sexual dichromatism remains unclear and, in general, the assumption of stronger sexual selection in lower latitudes is controversial (Cardillo, 2002; Dale et al., 2015). The another reason why birds can afford to be more colourful in tropics and at the same time not to be endangered by predators is based on the light conditions of the dense vegetation cover. The contrast of striking plumage colouration with the vegetation background can be very low and birds may not be so apparent.

The availability and diversity of food resources required for the creation of feather pigments and the complexity of the tropical environment and its role in signal elaboration are linked with high environmental productivity. We expected that overall colourfulness as well as particular plumage colours would show spatial patterns along the productivity gradient. Environmental productivity can directly affect yellow-orange-red plumage colouration through the availability of carotenoids from food resources (Hill, 2006; McGraw, 2006). Structural green-blue colouration, iridescence and colour saturation may be affected through adequate nutrition for resistance to parasitic infection or for good individual condition for colour creation. Melanin-based grey-brown-black colouration is also dependent on the intake of pigment precursors and minerals (Hill, 2006). In terms of the availability and diversity of food resources, the more productive environments should host more colourful birds. Concerning environmental diversity, we can think about the signalling and cryptic function of plumage colouration. Both are the result of potentially antagonistic effects of sexual and natural selection, while the role of each selection prevails in different environments. The lower need to be cryptic and simultaneously the higher pressure on visual signal expression in more productive areas may lead to more conspicuous, more saturated or iridescent colouration. In addition, unproductive areas with sparse vegetation may select for pale grey-brown colouration as the cryptic display is required in open habitats. Cryptic colouration may also be enhanced by spottiness patterns which make the bird's body less noticeable against the background (Stevens & Merilaita, 2009). The arid unproductive environment may also have different requirements on the feather protection what may affect the overall colour expression.

In this study, we reviewed the colourful tropics hypothesis in birds. We aimed to examine general patterns in the spatial distribution of plumage colouration along a large-scale productivity gradient in South Africa. We focused on all breeding birds living in South Africa and Lesotho. We quantified colour characteristics reflecting pigment type, ornaments or sexual dichromatism. We also parameterized spectral properties of colours; saturation and brightness. For examination of overall colourfulness, we used a computer model-based and human-based approach.

Materials and methods

Species distribution data

The comprehensive information on the distribution of bird species across South Africa and Lesotho were taken from the Southern African Bird Atlas Project (SABAP), which surveyed therein living birds mainly between years 1987 and 1992 (Harrison et al., 1997). All birds were recorded at the quarter-degree (~25 × 25 km) spatial resolution and the avian composition in each grid cell was considered as a local assemblage. The dataset used in the analyses included 579 species breeding within the study area. Marine, rarely occurring non-breeding vagrants, marginal (occurring in 5 or less grid cells) and bird species escaped from captivity, we did not include in the dataset. For each grid cell, we also obtained data on environmental productivity and the mean values/proportions of colour characteristics of bird assemblages.

Environmental productivity

For each grid cell, we obtained the Normalized Difference Vegetation Index (hereafter NDVI) as the estimate of environmental productivity, based on the spectral radiance of vegetation. Average monthly maxima of NDVI from the period 1982 - 2004 were taken from the Africa Data Dissemination Service data set provided by the U. S. Geological Survey (http://iridl.ldeo.columbia.edu/SOURCES/.USGS/.ADDS). For each grid cell, the value of the month with the highest NDVI was used as the estimate of maximum environmental productivity (hereafter $NDVI_{max}$) (Fig. 1). NDVI describes the 'greenness' of vegetation and it is closely correlated with rainfall, total green biomass and net primary productivity (Goward & Dye, 1987; Chong, Mougin, & Castellu-Etchegorry, 1993; Paruelo, Epstein, Lauenroth, & Burke, 1997; Schmidt & Karnieli, 2002). It has been also shown that variation in this index reflects the differences in the amount of food availability, such as arthropod abundance, to birds breeding over large spatial scales (Lassau & Hochuli, 2008; Lafage, Secondi, Georges, Bouzillé, & Pétillon, 2014).

Avian colour characteristics

For each local assemblage, we calculated the mean value of each colour trait or the proportion of species with the certain trait value. We estimated species specific properties of bird plumage using illustrations of breeding males from the *Birds of Southern Africa* atlas (Sinclair, Hockey, Tarboton, Hayman, & Arlott, 2002). We determined 13 characteristics of plumage colouration for all 579 bird species, from which 9 were binary coded categories (present/absent) and 4 continuous variables:

- Five categories for colour combinations with regard to pigment type or the character of production: (1) yellow-orange-red, (2) green-blue, (3) predominantly black, (4) black and white, and (5) grey-brown.
- Four categories for colour patterns: (1) spottiness, (2) black tips of tail and wings, (3) iridescence, and (4) sexual dichromatism.
- Four quantitative colour traits: (1) colourfulness assessed by human evaluation and (2) by the computer model, (3) saturation (the degree of purity in the hue), and (4) brightness (relative lightness and darkness).

Species fell into that category, whose colour characteristic they markedly exhibited. A species could be included into more than one category, with the exception of pigment type, which was classified by five mutually exclusive categories. With the exception of some colour patterns (spottiness and black tips), we did not take into consideration the shape of the colour patches or their position. The presence of black colouration was divided into two categories (black and white and predominantly black), as the combination of black colour and white colour is highly contrasting in comparison with purely black colour.

For determination of colourfulness (variegation/multicolouration), we applied two approaches; (1) human evaluation and (2) the RGB/HSV computer model. For estimation of colourfulness with the help of human respondents, we selected 100 representatives of all colour phenotypes, regardless of their taxonomic affiliation. The reduced set of species included only males in breeding plumage, shown from a side view and in same size. All pictures of selected species were cut from the atlas and placed on white separate cards of 10 × 10 cm. Subsequently, 37 respondents were asked to rank birds according to increasing "colourfulness", without *a priori* definition of this term. In this way, an average rank of colourfulness of each colour phenotype was obtained and these values were assigned to remaining species of similar colour phenotype. The colourfulness was also determined by the computer model, as well as saturation and brightness. For this purpose, all studied bird species were scanned from the atlas at the resolution 600 DPI. In order to eliminate incorrect pixels caused by resolution and quality of scanning, Gaussian defocusing of radius $r = 3$ was applied on the illustrations in the program GIMP 2.6.11. For each individual, 10 body regions were specified, located on bill, forehead, crown, cheek, breast, abdomen, back, rump, wing, and tail. The measured surface within each body region was a square of 25 × 25 pixels, that was chosen and located to best represent local colouration. If there were more colours within the region, the square was placed so that each colour was represented proportionally. For each body region, we obtained the values of hue (for colour determination), saturation, brightness, and the number of different colours. We defined 9 reference colours: red, orange, yellow, green, blue, purple, pink, brown, and greyscale (a scale from white to black). Each colour was evaluated at three levels of saturation (light, middle, deep). For each saturation level, RGB values were established from randomly selected illustrations in the program Adobe Photoshop CS3 and in the RGB program. Value establishment at each level was repeated several times. The RGB values were then transformed by the specific algorithm to the HSV values. Based on the HSV model, a mean value for each colour (hue) was determined and then around it the limits of its colour range were determined as the arithmetic mean of the means of two adjacent colours on a colour scale. The limits were not located symmetrically around the mean as the distances between the means of reference colours varied. For identification of colourless shades (greyscale), we established the value of saturation less than 0.2. The shades of grey were distinguished on a brightness scale, which was divided into three equal segments; for white, grey, and black colour. Brown and orange differed only slightly in hue values, so the brightness value was used as the distinguishing factor. Based on the precise definition of all reference colours, we were able to determine colours within each body region. The values of saturation and brightness were assigned to the particular colours on the basis of their predefined intervals. Finally, we calculated the number of different colours in each bird and its average saturation and brightness. The number of colours on the species body was a measure of its colourfulness (multicolouration). It is important to note that due to the different methods of determination of colourfulness, we obtained two different variables of this bird plumage characteristic. In the case of human evaluation, colourfulness meant something in terms of striking colouration or conspicuousness, while computer model evaluation basically meant multicolouration.

The patterns of geographical variation in all 13 plumage colour characteristics are shown in maps (Fig. 2). The maps were performed in the program SAM v4.0 (Rangel, Diniz Filho, & Bini, 2010).

Statistical analysis

We took three approaches to identify relationships between the colour characteristics and environmental productivity:

1) First, we applied a three-table ordination analysis, an extended co-inertia analysis known as RLQ analysis, which connects environmental variables with species traits through the species composition (Dolédec, Chessel, Braak, & Champely, 1996; Ribera, Dolédec, Downie, & Foster, 2001; Dray, Chessel, & Thioulouse, 2003; Dray & Legendre, 2008). This statistical procedure is symmetrical in the sense that it does not emphasise environmental or species trait data (Cleary et al., 2007; Rachello-Dolmen & Cleary, 2007; Voogd & Cleary, 2007). The analysis is also not affected by the collinearity among variables (Dray et al., 2003). The principle of the mathematical model consists in the eigenvalue decomposition of the cross-matrix providing the ordination axes onto which projected sites and species have maximal covariance, and thus present the best combination of their maximal correlation and explained variability (Dolédec et al., 1996; Choler, 2005; Thuiller, Richardson, Rouget, Procheş, & Wilson, 2006). In this approach, each dataset was first analysed through a factorial analysis, in order to compare the results with those of the three-table join analysis. The distance matrix of the environmental productivity variable was analysed by principal coordinate analysis (PCoA), using the Euclidean metric. The species composition matrix was analysed by correspondence analysis (CA). The trait distance matrix of the whole dataset of colour variables was analysed by principal coordinate analysis (PCoA). As the dataset of colour traits included different statistical types of variables, we computed a distance matrix with the mix-variables coefficient of distance (Pavoine, Vallet, Dufour, Gachet, & Daniel, 2009) based on a generalization of Gower's distance. In the case of a common analysis of the whole trait set, we considered that some traits could be linked together by evolution and, therefore, they cannot necessarily be treated as independent entities.
2) In the second step we used the forth-corner statistics (Legendre, Galzin, & Harmelin-Vivien, 1997), with the aim to quantify and test the significance of the relationships. For the purpose of this study, it was appropriate to use a test based on a null model 4 (Dray & Legendre, 2008). The null hypothesis assumes that the species are distributed with respect to their preferences to the given environmental conditions, but regardless of which traits they dispose. On the contrary, rejecting the null hypothesis supports the ecological hypothesis that the species are distributed depending on their adaptations (traits) to the environmental conditions, while the preferences of the species for site conditions are not questioned. Under this model, the species richness per site is kept constant (Dray &

Legendre, 2008). We performed the fourth-corner analysis (based on the sum of all eigenvalues in the cross-matrix; 999 permutations) for each trait separately (trait distance matrixes), as this test related with the fourth-corner approach allows also estimate the performance of single-variable × single-trait analyses (Vallet, Daniel, Beaujouan, Rozé, & Pavoine, 2010). However, since the fourth-corner test has not been developed yet for distance matrixes, we adapted the testing principles as proposed in Pavoine et al. (2009) and Vallet et al. (2010).

3) In the third approach we took into account a phylogenetic relatedness of studied species. We used the phylogeny of Jetz, Thomas, Joy, Hartmann, and Mooers (2012) obtained from A global phylogeny of birds (http://birdtree.org/) with Hackett et al. (2008) backbone constraint in order to generate 100 random phylogenetic trees. We assumed that species traits could be correlated through common evolutionary history, closely related taxa are therefore more likely to share the same characteristics than distant ones (Logue & Hall, 2014; Odom, Omland, & Price, 2015). To incorporate the phylogenetic relatedness among taxa we performed a phylogenetic generalized least squares analysis (PGLS) (Martins & Hansen, 1997) separately for each quantitative trait variable and generalized estimating equations analyses (GEE) (Paradis & Claude, 2002) for qualitative trait variables. The PGLS regression model includes a variance-covariance matrix that describes the phylogenetic structure, determined by topology and branch lengths, and that shoud be considered to be autocorrelation variable in the model. The maximum-likelihood value of the strength of phylogenetic signal (lambda) is estimated by fitting a PGLS model with different values of lambda applied to the variance-covariance matrix in order to achieve the highest log-likelihood (Pagel, 1999; Freckleton, Harvey, & Pagel, 2002). The GEE model treats with the phylogenetic dependency as a nuisance parameter to be corrected. We fitted univariate GEE models including each trait variable alone to determine its association with $NDVI_{max}$. We specified a logit link function and binary error structure.

All analyses and graphics were completed in R software (R Development Core Team 2017; http://www.r-project.org/).

Results

Environmental productivity and colour characteristics

The association between the prominent spatial gradient in environmental productivity and bird colouration (based on all colour characteristics) was very strong: the global fourth-corner test was strongly significant ($p < 0.001$). This means that the geographical pattern in the biggest differences among birds on the basis of all their colour characteristics was strongly correlated with the gradient in environmental productivity. In other words, the appearance of the species assemblages, assessed on the basis of all colour characteristics, varied most rapidly along the productivity gradient. 69% of the overall variability in measured colour characteristics was explained by the environmental variable (Tab. 1). The environmental productivity seems to control distributions of species according to their colour adaptations.

The main axis of the co-inertia RLQ analysis extracted the whole variance (coinertia) of the cross-matrix that joins all colour characteristics of birds and the environmental productivity variable of the sites (Tab. 1). Because the RLQ analysis represents the partial ordination of the environmental variable of the sites, species composition, and the colour traits of the species, the proportion of variance attributed to each matrix was compared to that resulting from their separate analyses. The axis of the RLQ analysis accounted for 69% of the potential variability explained by the first axis of the separate PCoA of the colour characteristics. Since there was a single environmental variable, the RLQ axis took into account the whole potential variability of the single main axis of the separate PCoA of the distance matrix based on environmental productivity. The new sets of sites and species scores had a correlation of 0.129 along the RLQ axis, which represented 21.5% of the maximum possible correlation between sites and species, given by the square root of the first eigenvalue of the CA of the species composition table. The covariance between the new sets of scores for the sites and species, which is optimized by the RLQ axis, was equal to 0.003.

The qualitative and quantitative colour characteristics were ordered along the main axis of the RLQ analysis according to their weights in the linear combination that provided the coordinates of species (Fig. 3). The RLQ axis represented the gradient of environmental productivity, as the axis possessed total variance of the main PCoA axis of this environmental variable. The RLQ axis accounted for a considerable gradient in colour traits given by the differences between colourful birds occurring in productive habitats and pale birds living in unproductive environments. The vivid species with green-blue, iridescent, yellow-orange-red, and black high saturated plumage colouration obtained the highest positive scores on the RLQ axis, related to the productive environment. On the opposite side of the RLQ axis, the species in which prevailed grey-brown lighter colouration and black tips of tail and wings, obtained the lowest (negative) scores, linked to the environment with low productivity. Sexual dichromatism, black and white combination, spottiness pattern and multicolouration (the number of different colours) were not markedly located at either end of the RLQ axis, suggesting that birds with these plumage characteristics were more equally distributed across the study area (Fig. 3). These results are in accordance with depicted geographical patterns in colour characteristics (Fig. 2). Maps (Fig. 2) show weaker and stronger spatial patterns along the productivity gradient (Fig. 1).

Table 1. Results of the RLQ analysis

RLQ analysis			
Analysis	Variance RLQ axis	Covariance RLQ axis	Correlation RLQ axis
R/RLQ	0.029	0.003	0.129
Q/RLQ	0.019		

Separate analyses		
Analysis	Variance axis 1	Variance axis 2
R/PCoA	0.029	
L/CA	0.361	0.224
Q/PCoA	0.027	0.019

RLQ summary	
Analysis	Explained variance (%) RLQ axis
R/RLQ	100
L/RLQ	21.5
Q/RLQ	69

R/RLQ and Q/RLQ in RLQ analysis – variance (inertia) of the site variable and species traits, respectively, possessed by the RLQ axis; covariance and correlation between the set of species and sites scores along the RLQ axis. R/PCoA - principal coordinate analysis of the distance matrix of the environmental productivity variable; L/CA - correspondence analysis of the species composition table; Q/PCoA - principal coordinate analysis of the distance matrix of colour characteristics. RLQ summary shows the comparison of the RLQ analysis with the separate analyses and the percentage of total variance accounted for by the RLQ axis.

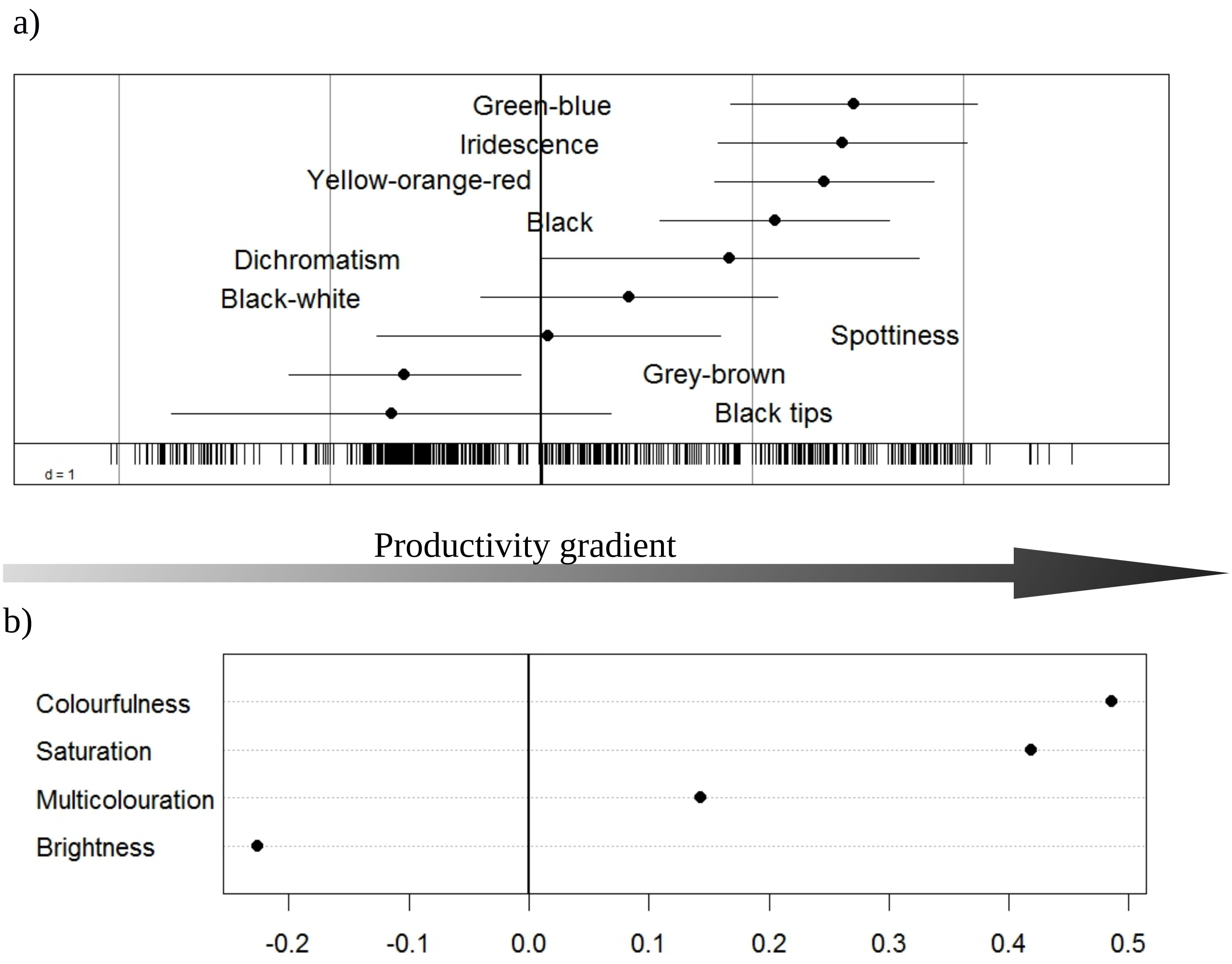


Figure 3. Graphical projection of the colour characteristics on the ordination axis from the RLQ analysis maximizing covariance among three data sets. (a) The categorical characteristics of colouration are located at the average coordinates of the species that has them. The length of segments corresponds to the standard deviation of the scores of the species that has given characteristic. The vertical lines present the position of species at the average score of the sites in which they occur. (b) Pearson correlations between the quantitative colour traits and the coordinates of the species along the RLQ axis. The right part of the axis is associated with productive environments, the left with unproductive environments.

The permutation tests of the fourth-corner analysis

Individual characteristics of bird colouration with significant correlations with the higher values of environmental productivity were: yellow-orange-red, green-blue, whole black, and colourfulness evaluated by respondents. Colour characteristics that were significantly and negatively associated with the lower values of environmental productivity were: grey-brown, black tips, and brightness (Tab. 2). Although iridescence and saturation showed apparent spatial patterns and both characteristics were markedly positioned at the end of the RLQ axis related to high productivity, it turned out that their association with environmental productivity proved not to be significant. The graphical representation of the permutation tests is in Fig. 4.

We used the fourth-corner statistic to test the hypothesis that birds developed their colour traits in accordance with environmental conditions. The geographical patterns of results of the permutation tests showed that bird assemblages non-randomply exceed in a certain colour characteristic at a certain level of productivity (Fig. 4).

Table 2. Summary of the tests for the links between colour characteristics and productivity

Colouration	Deviation	P-value	Conclusion
Yellow-orange-red	3.75	0.013	S
Green-blue	3.47	0.015	S
Whole black	7.32	0.002	S
Black and white	-0.47	0.573	NS
Grey-brown	9.64	0.001	S
Spottiness	-0.49	0.576	NS
Black tips	3.50	0.017	S
Iridescence	1.63	0.066	NS
Dichromatism	-0.40	0.202	NS
Colourfulness	3.22	0.02	S
Multicolouration	-0.05	0.339	NS
Saturation	1.05	0.115	NS
Brightness	3.29	0.018	S

Colourfulness – colourfulness evaluated by respondents, Multicolouration – colourfulness evaluated by the computer model; S – significant result, NS – non-significant result. Deviation - the deviation from theoretical values represents the distance between the observed value of the statistic and the theoretical values established by random permutations. A positive/negative deviation means that the statistic is higher/lower than expected. The P-value is calculated as the proportion of theoretical values that are higher or equal to the observed value of the statistic (sum of eigenvalues of the RLQ).

Examination of phylogenetic signal in the relationships between productivity and colour characteristics

Results of both GEE (for categorical characteristics) and PGLS (for quantitative characteristic) models revealed that phylogenetic signal in bird plumage colouration was very strong in most colour characteristics (Tab. 3 and 4). Only whole black colouration, brightness and colourfulness (conspicuousness) may represent convergent adaptations to productive tropical conditions. Other colour characteristics apparently exhibited similar spatial patterns in phylogenetic relatedness and colour characteristics.

Table 3. Results of GEE models for categorical colour characteristics

Categorical variables	Percentage of significant results
Yellow-orange-red	5
Green-blue	0
Whole black	69
Black and white	4
Grey-brown	0
Spottiness	0
Black tips	2
Iridescence	0
Dichromatism	0

Table 4. Results of PGLS models for quantitative colour characteristics

Quantitative var.	Percentage of sig. results	P-values	AIC	loglik
Colourfulness	63	0.020-0.106	2275-2283	-1138-(-1133)
Multicolouration	0	0.538-0.851	274.8-277.2	-134.6-(-133.4)
Saturation	0	0.054-0.310	-948.3-(-934.8)	471-478.1
Brightness	66	0.025-0.087	-999.4-(-988.6)	498.3-503.7

Percentage of significant results means the number of models (of the total 100) in which the p-value was lower or equal to 0.05; P-values represents range of p-values (min - max value); AIC represents interquartile range (1. - 3. quartile; the middle 50% of values) of AIC values for all 100 models; loglik means log likelihood and represents interquartile range of this value; We fitted models derived from the Brownian motion model by multiplying the off-diagonal elements (the covariances) by lambda. The variances are thus the same as for the Brownian motion model.

Discussion

We found striking geographical patterns in avian plumage colouration across South Africa that were strongly linked to the environmental productivity gradient. Our results provide strong support for the hypothesis that birds are more colourful in tropics. More colourful species, yellow-orange-red species (having carotenoids in feathers), green-blue species or predominantly black occurred mainly in highly productive habitats such as humid savanna, woodlands and forests in the north-east of South Africa. On the contrary, pale grey-brown species and species with brighter feathers and with black tips of tail and wings occupied arid inhospitable habitats in the west. Other characteristics such as black and white combination, spottiness, saturation, iridescence and sexual dichromatism exhibited weak trends along the gradient of productivity, but they did not prove as significant.

There are several hypotheses that can provide explanations for the revealed relationships between geographical variability in environmental productivity and plumage colour characteristics. Their arguments are usually based on the concept of trade-offs between different selection pressures. Our results showed that more colourful birds occur in the area of the whole eastern and north-eastern part of South Africa, which comprises the most productive habitats. Selection for signalling needs through colour conspicuousness in these productive habitats could be a consequence of stronger female mate choice (Badyaev & Hill, 2003). High environmental productivity may increase the density of individuals and so potential competitors for mates and resources (Verner & Willson, 1966). However, environmental productivity may control many aspects of reproductive life-history strategies and social organization (Emlen & Oring, 1977) that may not be related to abundance. In productive tropical environments, stable food resources select for strong long-term territoriality, and subsequent rare opportunities to establish new breeding vacancies promote cooperative breeding (Pen & Weissing, 2000), polygyny and strong intrasexual competition (Emlen & Oring, 1977). Increasing intensity of different selection pressures leads to the requirements for demonstrating individual quality as a mate and/or territory competitor (Badyaev & Hill, 2003). And high environmental productivity allows to obtain sufficient resources for elaboration of that signals of quality. Alternatively, sexual selection pressure may be increased due to increasing breeding synchrony in high seasonal environments (Friedman & Remeš, 2016). In South Africa, environmental productivity is strongly correlated with its seasonality (Hořák, Tószögyová, &

Storch, 2015). Thus, elaboration of colourful plumage in birds in the study area may be the result of various mechanisms.

Predation rates may be higher in tropical regions (McKinnon et al., 2010), what would have the opposite effect on the need to be visible. Nevertheless, as we showed in the previous study (Hořák et al., 2011), this is not the case in this study area, where predation risk seems to be higher in arid unproductive habitats. The pattern of greater colourfulness in productive environments may thus be the outcome of the prevailing sexual selection pressure over the predation pressure. On the contrary, the prevailing predation pressure on adult birds in more open habitats leads to cryptic colouration. Our results confirmed that most species have inconspicuous grey-brown colouration in unproductive areas of semi-deserts and, to a lesser extent, also in grasslands. We initially assumed that disruptive colouration of spottiness could also be associated with arid open habitats as this pattern acts as an anti-predator adaptation (Endler, 1992). However, spottiness can also play a role in communication to attract females. Whether spottiness has a signalling or cryptic function depends on whether it is regular or irregular (Somveille, Marshall, & Gluckman, 2016). However, there is no evidence for association between habitat type and regular and irregular spottiness (Somveille et al., 2016). We did not distinguish spottiness on the basis of its regularity, and our results also showed no spatial trend in this colour characteristic. Probably, for the same reason that we did not distinguish between countershading and other black and white patterns, the cryptic and signalling functions of colouration were mixed, and the black and white pattern did not show any spatial trend in the study area.

If we expect stronger sexual selection with subsequent competition for potential mates, then it should lead to a greater extent of dichromatism between sexes (Endler, 1993). Nevertheless, the higher occurrence of dichromatism in tropical regions is not confirmed by other authors (Bailey, 1978; Cardillo, 2002), and we also did not find any spatial gradient. On the other hand, sexual dichromatism may be more common in temperate regions than in tropics (Bailey, 1978). Both sexes are more colourful and ornamented in tropical environments due to evolutionary cohesion in conspecific male and female colour elaboration (Dale et al., 2015). Alternatively, female conspicuousness in tropics can be the outcome of strong competition for breeding-related resources, leading to the selection pressure on the signalling function in both sexes. On the contrary, strong sexual selection on males results in greater male colourfulness and reduced female ornamentation (Dale et al., 2015). The existence of the geographical gradient in sexual dichromatism is due to conflicting evidence still unresolved.

In addition to productivity or diversity of environments, variation in light environments across differently productive habitats may also be responsible for spatial patterns in avian colouration. Light environment hypothesis claims that the effectiveness of visual communication through colouration is dependent on the ambient light spectrum (Théry, 2001). For colour signalling in intra- and interspecific interactions, species tend to use colours that match the ambient light irradiance peak to maximize brightness contrast and colours that are poor in the background reflectance spectra to maximize colour contrast. Alternatively, to be inconspicuous as a part of crypsis, birds adopt the opposed contrast-reducing strategy (Endler, 1990; Théry, 2001). The environments differ in light wavelengths transmitted through vegetation, which considerably modifies conspicuousness of visual signals (Endler, 1990; Bradbury & Vehrencamp, 1998; Théry, 2001). Good transmission efficiency of particular colour signal in one environment does not mean that the same signal would act in another environment, because in the context of another light environment, the visual expression of this colour may be suppressed or changed (Endler, 1993). In the light of these predictions, we expected the differences in spatial distribution of particular colours and colour characteristics across differently productive habitats.

Since environmental productivity is not equally distributed across the study area and the light conditions of vegetation vary, conspicuousness will be realized in different ways, by elaboration of different pigments/colours in feathers. We showed that carotenoids (yellow-orange-red) are utilized in a dense canopy of the productive eastern woodlands and forests (KwaZulu-Natal and Mpumalanga). Endler (1993) and Théry (2001) predicted the same trend that species inhabiting a relatively closed environment, tend to use long wavelength colours, such as red and orange, as these colours dominate in a part of the ambient light spectrum transmitted through leaves and simultaneously contrast well against the surrounding vegetation. We found that green-blue of structural colouration occurs mainly in species inhabiting lighter canopies of woodlands and northern less productive savannas (Limpopo). This finding was also consistent with the study of mentioned authors who claimed that colour signal within woodland shade should be blue, blue-green or UV to maximize brightness contrast (total reflectance). According to Marchetti (1993), bird feathers in this environment should also be brighter and reflect more light in comparison with species living in relatively open habitats, because the overall luminescence is lower in dense vegetation. The results of the study by McNaught and Owens (2002) and also our results were inconsistent with this prediction, as the brighter species occur in open areas with sparse vegetation. Saturation of colours can also potentially play a role in visibility (Endler, 1990). High saturated plumage will be less sensitive to changes in ambient light than those with low saturation and should therefore be used in species that need to maintain their colour contrast independent of light conditions. Species that need to be cryptic in various habitats should have low saturated plumage which is able to adjust relatively to background colour fluctuations (Endler, 1993, 1997). Although, we found that plumage colour saturation was not significantly related to environmental productivity, there is still a weak spatial pattern in saturation with higher values in productive habitats. It is possible that birds modify their visual contrast with the background through the changes in colour intensity but only in a specific environment (e.g. in the vertical light gradient in high tree canopy) (Endler, 1993, 1997). Dense vegetation in tropics limits visibility to small distances, what may represent suitable conditions for iridescent birds. Iridescent colours reflect light only at relatively small angles, proper angle and distance are needed for visibility (Bailey, 1978). Shade and dense foliage allow birds to show this striking signal only to recipients in close distance while they can be hidden from predators. In this study, geographical patterns in iridescence are in accordance with this prediction, but they are not significantly associated with geographical variability in environmental productivity.

Another explanation for environment-related variation in plumage colouration is based on the intake of different amounts and types of nutrients for pigment creation, as different environments are able to provide specific food resources (McGraw, Hill, Stradi, & Parker, 2001; Hill, Inouye, & Montgomerie, 2002). Birds (as well as all vertebrates) cannot synthesize carotenoid pigments *de novo* (Brush, 1981), and thus the creation of pigments is highly dependent on the access to their dietary precursors (Goodwin, 1984; Hill, 1992, 1996), which differs along the productivity gradient (Olson & Owens, 1998). Woodlands and forests can provide sufficient resources for carotenoid-based colouration as there is the stable availability of insect and fruits. In accordance with these assumptions, our results showed that birds with carotenoid pigments in feathers (yellow-orange-red) are associated with productive habitats. Similarly, production of melanin-based (grey-brown-black) and structural (green, blue, purple, ultraviolet, and iridescence) colouration is dependent on nutrition (Keyser & Hill, 1999, 2000; McGraw, Mackillop, Dale, & Hauber, 2002). Birds displaying melanin-based or structural colouration may require an environment with low nutritional constraints. However, production of melanin-based and structural colouration may not be directly affected by dietary precursors, but indirectly through individual condition dependent on nutrition (Hill, 2006). We found that green-blue birds inhabit productive woodlands, but birds with iridescent feathers are not associated with the productivity gradient, even though they show a spatial pattern.

The environment-dependent need for feather reinforcement and protection may also play a role. We found that the occurrence of whole black birds and darker (lower brightness) birds increases with the productivity gradient. To the similar conclusions came Zink and Remsen (1986) who found that birds tend to have darker plumage in areas of high relative humidity and called it as Gloger's rule. Possible explanation is based on the need for camouflage or the higher resistance of dark eumelanic feathers to bacterial load, probably higher in humid areas (Burtt, 1981; Burtt & Ichida, 2004). The presence of melanin pigments in feathers also reduces their abrasive degradation, and it is expected to be preferred in arid environments (Burtt, 1979; Barrowclough & Sibley, 1980; Burtt, 1981; Bonser, 1995). This can be a reason why birds with black tips of wings and tail occur mainly in non-productive arid areas, as our results confirmed.

We estimated colourfulness by two different measurements, which gave different results. The RGB/HSV computer model evaluated the degree of colourfulness in terms of the number of different colours on a bird's body, but this variable did not show any obvious geographical pattern and thus no correlation with productivity. On the contrary, colourfulness estimated by the respondents correlated significantly and positively with productivity. *A posteriori*, we found that people evaluated bird colourfulness on the basis of two different criteria: (i) species bearing several conspicuous colours or (ii) species having only few but strong contrasting colours (e.g. yellow-black, red-green). The latter includes, for example, swallow-tailed bee-eater (*Merops hirundineus*), crested barbet (*Trachyphonus vaillantii*), lilac-breasted roller (*Coracias caudatus*), and sunbirds (*Nectarinia* spp.). In both cases, people considered a bird to be colourful if it was conspicuous. Consequently, a comparison of the computer-based and human-based approaches revealed that not the number of different colours on the bird's body, but rather conspicuousness of individual colours was higher in productive environments.

Our large-scale approach has certain limitations related to avian visual perception and environmental context. Although avian and human visual perception is different (some birds are sensitive to UV light (Chen, Collins, & Goldsmith, 1984; Ödeen & Håstad, 2003; Carvalho, Cowing, Wilkie, Bowmaker, & Hunt, 2007)) (Endler, 1990; Bennett & Cuthill, 1994; Cuthill, Partridge, & Bennett, 2000; Endler & Mielke, 2005), birds do not visually interact only within their taxon. Birds are also, for instance, predators of other taxa and simultaneously prey of another, while all taxa may have mutually different visual ability. Human perception of colours and colourfulness may therefore be appropriate for plumage colour determination, since human spectral sensitivity fully encompasses the sensitivity range of many birds (except these UV sensitive) (Bleiweiss, 2004). Another problem may be context-dependent colours and transmission of visual signal. The role of environmental context is enormous (daytime, season, weather, microhabitats, stratification of vegetation, and visual perception of interacting species) and the relevance of particular colours differs even among particular habitats within the geogpraphical range or among particular species within one place (diurnal or nocturnal bird, birds of different vegetation floors). Nevertheless, the aim of our study was to reveal rough geographical variability in colouration, hence including the context of surrounding conditions of particular microhabitats or human-independent colour perception would not significantly increase the reliability of the study.

References

Allen, J. A. (1877). *The influence of physical conditions in the genesis of species,* Vol. 1, Smithsonian Institution Press.

Badyaev, A. V., & Hill, G. E. (2003). Avian sexual dichromatism in relation to phylogeny and ecology. *Annual Review of Ecology, Evolution, and Systematics*, 34, 27–49.

Bailey, S. F. (1978). Latitudinal gradients in colors and patterns of passerine birds. *The Condor, 80*(4), 372–381.

Bailey, S.-A., Horner Devine, M. C., Luck, G., Moore, L. A., Carney, K. M., Anderson, S., … Fleishman, E. (2004). Primary productivity and species richness: relationships among functional guilds, residency groups and vagility classes at multiple spatial scales. *Ecography*, *27*(2), 207–217.

Baker, R. R., & Parker, G. A. (1979). The evolution of bird coloration. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences*, *287*(1018), 63–130.

Barrowclough, G. F., & Sibley, F. C. (1980). Feather Ppgmentation and abrasion: Test of a hypothesis. *The Auk*, *97*(4), 881–883.

Bennett, A. D. T., & Cuthill, I. C. (1994). Sexual selection and the mismeasure of color. *American Naturalist*, *144*(5), 848.

Bergmann, C. (1847). *Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Größe* , Vol. 3, Göttingen.

Bleiweiss, R. (2004). Ultraviolet pumage reflectance distinguishes sibling bird species. *Proceedings of the National Academy of Sciences of the United States of America*, *101*(47), 16561–16564.

Bonser, R. H. C. (1995). Melanin and the abrasion resistance of feathers. *The Condor*, *97*(2), 590–591.

Bradbury, J. W., & Vehrencamp, S. L. (1998). *Principles of animal communication,* Oxford University Press.

Brush, A. H. (1981). Carotenoids in wild and captive birds. In Bauernfeind J. C. (Eds.), *Carotenoids as colorants and vitamin A precursors,* (539–562). Academic Press, New York.

Burtt, E. H. (1979). Tips on wings and other things. In Burtt, E. H. (Eds.), *The behavioural significance of colour*, (75–100). New York: Garland Press.

Burtt, E. H., & Ichida, J. M. (2004). Gloger's rule, feather-degrading bacteria, and color variation among song sparrows. *The Condor*, *106*(3), 681-686.

Burtt, E. H. (1981). The adaptiveness of animal colors. *BioScience*, *31*(10), 723–729.

Burtt, E. H. (1986). An analysis of physical, physiological, and optical aspects of avian coloration with emphasis on wood-warblers. *Ornithological Monographs*, (38), 1–126.

Butcher, G. S., & Rohwer, S. (1989). The evolution of conspicuous and distinctive coloration for communication in birds. In Power, D. M. (Eds.), *Current Ornithology*, (51–108), Springer, Boston, MA.

Cardillo, M. (2002). The life-history basis of latitudinal diversity gradients: how do species traits vary from the poles to the equator? *Journal of Animal Ecology*, *71*(1), 79–87.

Carvalho, L. S., Cowing, J. A., Wilkie, S. E., Bowmaker, J. K., & Hunt, D. M. (2007). The molecular evolution of avian ultraviolet- and violet-sensitive visual pigments. *Molecular Biology and Evolution*, *24*(8), 1843–1852.

Chen, D.-M., Collins, J. S., & Goldsmith, T. H. (1984). The ultraviolet receptor of bird retinas. *Science*, *225*(4659), 337–340.

Choler, P. (2005). Consistent shifts in alpine plant traits along a mesotopographical gradient. *Arctic, Antarctic, and Alpine Research*, *37*(4), 444–453.

Chong, L. S. D., Mougin, E., & Castellu-Etchegorry, J. P. (1993). Relating the Global Vegetation Index to net primary productivity and actual evapotranspiration over Africa. *International Journal of Remote Sensing*, *14*(8), 1517–1546.

Cleary, D. F. R., Boyle, T. J. B., Setyawati, T., Anggraeni, C. D., Loon, E. E. V., & Menken, S. B. J. (2007). Bird Species and traits associated with logged and unlogged forest in borneo. *Ecological Applications*, *17*(4), 1184–1197.

Cuthill, I. C., Partridge, J. C., & Bennett, A. T. D. (2000). Avian UV vision and sexual selection. In Espmark, Y., Amundsen, T., & Rosenqvist, G. (Eds.), *Animal Signals: Signalling and Signal Design in Animal Communication*, (87-106). Tapir Academic Press, Trondheim, Norway.

Dale, J., Dey, C. J., Delhey, K., Kempenaers, B., & Valcu, M. (2015). The effects of life history and sexual selection on male and female plumage colouration. *Nature*, *527*(7578), 367–370.

Dalrymple, R. L., Kemp, D. J., Flores   Moreno, H., Laffan, S. W., White, T. E., Hemmings, F. A., … Moles, A. T. (2015). Birds, butterflies and flowers in the tropics are not more colourful than those at higher latitudes. *Global Ecology and Biogeography*, *24*(12), 1424–1432.

Delhey, K., Smith, J., & Peters, A. (2013). Colour-variable birds have broader ranges, wider niches and are less likely to be threatened. *Journal of Evolutionary Biology*, *26*(7), 1559–1568.

Dolédec, S., Chessel, D., Braak, C. J. F. ter, & Champely, S. (1996). Matching species traits to environmental variables: a new three-table ordination method. *Environmental and Ecological Statistics*, *3*(2), 143–166.

Dray, S., Chessel, D., & Thioulouse, J. (2003). Co-inertia analysis and the linking of ecological data tables. *Ecology*, *84*(11), 3078–3089.

Dray, S., & Legendre, P. (2008). Testing the species traits-environment relationships: The fourth-corner problem revisited. *Ecology*, *89*(12), 3400–3412.

Emlen, S. T., & Oring, L. W. (1977). Ecology, sexual selection, and the evolution of mating systems. *Science*, *197*(4300), 215–223.

Endler, J. A. (1978). A predator’s view of animal color patterns. In Hecht, M. K., Steere, W. C., & Wallace, B. (Eds.), *Evolutionary Biology*, (319–364), Springer, Boston, MA

Endler, J. A. (1990). On the measurement and classification of colour in studies of animal colour patterns. *Biological Journal of the Linnean Society*, *41*(4), 315–352.

Endler, J. A. (1992). Signals, signal conditions, and the direction of evolution. *The American Naturalist*, *139*, 125–153.

Endler, J. A. (1993). The color of light in forests and its implications. *Ecological Monographs*, *63*(1), 2–27.

Endler, J. A. (1997). Light, behavior, and conservation of forest-dwelling organisms. In Clemmons, J. R., Buchholz, R. (Eds.), *Behavioral approaches to conservation in the wild*. United Kingdom: Cambridge University Press.

Endler, J. A., & Mielke, P. W. (2005). Comparing entire colour patterns as birds see them. *Biological Journal of the Linnean Society*, *86*(4), 405–431.

Freckleton, R. P., Harvey, P. H., & Pagel, M. (2002). Phylogenetic analysis and comparative data: a test and review of evidence. *The American Naturalist*, *160*(6), 712–726.

Friedman, N. R., & Remeš, V. (2016). Global geographic patterns of sexual size dimorphism in birds: support for a latitudinal trend? *Ecography*, *39*(1), 17–25.

Friedman, N. R., & Remeš, V. (2017). Ecogeographical gradients in plumage coloration among Australasian songbird clades. *Global Ecology and Biogeography*, *26*(3), 261–274.

Gomez, D., & Théry, M. (2007). Simultaneous crypsis and conspicuousness in color patterns: Comparative analysis of a neotropical rainforest bird community. *The American Naturalist*, *169*(S1), 42–61.

Goodwin, T. W. (1984). *The biochemistry of the carotenoids,* Vol. 1, Chapman and Hall, London and New York.

Goward, S. N., & Dye, D. G. (1987). Evaluating North American net primary productivity with satellite observations. *Advances in Space Research*, *7*(11), 165–174.

Hackett, S. J., Kimball, R. T., Reddy, S., Bowie, R. C. K., Braun, E. L., Braun, M. J., … Yuri, T. (2008). A phylogenomic study of birds reveals their evolutionary history. *Science*, *320*(5884), 1763–1768.

Harrison, J. A., Allan, D. G., Underhill, L. G., Herremans, M., Tree, A. J., Parker, V., & Brown, C. J. (1997). *The atlas of southern African birds.*

Hill, G. E., Inouye, C. Y., & Montgomerie, R. (2002). Dietary carotenoids predict plumage coloration in wild house finches. *Proceedings of the*

Royal Society of London. Series B: Biological Sciences, *269*(1496), 1119-1124.

Hill, G. E. (2006). Environmental regulation of ornamental coloration. In Hill, G. E., McGraw, K. J. (Eds.), *Bird coloration, Vol. I: Mechanisms and measurements*, 507-560. Harvard University Press, Cambridge, MA.

Hill, G. E. (1992). Proximate basis of variation in carotenoid pigmentation in male house finches. *The Auk*, *109*(1), 1–12.

Hill, G. E. (1996). Redness as a measure of the production cost of ornamental coloration. *Ethology Ecology & Evolution*, *8*(2), 157–175.

Hořák, D., Sedláček, O., Tószögyová, A., Albrecht, T., Ferenc, M., Jelínek, V., & Storch, D. (2011). Geographic variation in avian clutch size and nest predation risk along a productivity gradient in South Africa. *Ostrich*, *82*(3), 175–183.

Hořák, D., Tószögyová, A., & Storch, D. (2015). Relative food limitation drives geographical clutch size variation in South African passerines: a large-scale test of Ashmole’s seasonality hypothesis. *Global Ecology and Biogeography*, *24*(4), 437–447.

Jetz, W., Thomas, G. H., Joy, J. B., Hartmann, K., & Mooers, A. O. (2012). The global diversity of birds in space and time. *Nature*, *491*(7424), 444–448.

Karr, J. R., & Brawn, J. D. (1990). Food resources of understory birds in central Panama: Quantifications and effects on avian populations. *Studies in Avian Biology*, *13*, 58–64.

Keyser, A. J., & Hill, G. E. (1999). Condition-dependent variation in the blue-ultraviolet coloration of a structurally based plumage ornament. *Proceedings: Biological Sciences*, *266*(1421), 771–777.

Keyser, A. J., & Hill, G. E. (2000). Structurally based plumage coloration is an honest signal of quality in male blue grosbeaks. *Behavioral Ecology*, *11*(2), 202–209.

Lafage, D., Secondi, J., Georges, A., Bouzillé, J.-B., & Pétillon, J. (2014). Satellite-derived vegetation indices as surrogate of species richness and abundance of ground beetles in temperate floodplains. *Insect Conservation and Diversity*, *7*(4), 327–333.

Lassau, S. A., & Hochuli, D. F. (2008). Testing predictions of beetle community patterns derived empirically using remote sensing. *Diversity and Distributions*, *14*(1), 138–147.

Legendre, P., Galzin, R., & Harmelin-Vivien, M. L. (1997). Relating behavior to habitat: Solutions to the fourth-corner problem. *Ecology*, *78*(2), 547-562.

Logue, D. M., & Hall, M. L. (2014). Migration and the evolution of duetting in songbirds. *Proceedings of the Royal Society B: Biological Sciences, 281*(1782).

Marchetti, K. (1993). Dark habitats and bright birds illustrate the role of the environment in species divergence. *Nature*, *362*(6416), 149.

Martins, E. P., & Hansen, T. F. (1997). Phylogenies and the comparative method: A general approach to incorporating phylogenetic information into the analysis of interspecific data. *The American Naturalist*, *149*(4), 646–667.

McGraw, K.J. (2006). Mechanics of carotenoid-based coloration. In Hill, G. E, McGraw, K. J. (Eds.), *Bird coloration, Vol. I: Mechanisms and measurements*, 177-242. Harvard University Press, Cambridge, MA.

McGraw, K. J., Hill, G. E., Stradi, R., & Parker, R. S. (2001). The influence of carotenoid acquisition and utilization on the maintenance of species-typical plumage pigmentation in male American goldfinches (Carduelis tristis) and Northern Cardinals (Cardinalis cardinalis). *Physiological & Biochemical Zoology*, *74*(6), 843.

McGraw, K. J., Mackillop, E. A., Dale, J., & Hauber, M. E. (2002). Different colors reveal different information: how nutritional stress affects the expression of melanin- and structurally based ornamental plumage. *Journal of Experimental Biology*, *205*(23), 3747–3755.

McKinnon, L., Smith, P. A., Nol, E., Martin, J. L., Doyle, F. I., Abraham, K. F., … Bêty, J. (2010). Lower predation risk for migratory birds at high latitudes. *Science*, *327*(5963), 326–327.

McNaught, M. K., & Owens, I. P. F. (2002). Interspecific variation in plumage colour among birds: species recognition or light environment? *Journal of Evolutionary Biology*, *15*(4), 505–514.

Ödeen, A., & Håstad, O. (2003). Complex distribution of avian color vision systems revealed by sequencing the SWS1 opsin from total DNA. *Molecular Biology and Evolution*, *20*(6), 855–861.

Odom, K. J., Omland, K. E., & Price, J. J. (2015). Differentiating the evolution of female song and male–female duets in the New World blackbirds: Can tropical natural history traits explain duet evolution? *Evolution*, *69*(3), 839–847.

Olson, V. A., & Owens, I. P. F. (1998). Costly sexual signals: are carotenoids rare, risky or required? *Trends in Ecology & Evolution*, *13*(12), 510–514.

Owens, I. P. F., Bennett, P. M., & Harvey, P. H. (1999). Species richness among birds: body size, life history, sexual selection or ecology? *Proceedings of the Royal Society B: Biological Sciences*, *266*(1422), 933.

Pagel, M. (1999). Inferring the historical patterns of biological evolution. *Nature*, *401*(6756), 877–884.

Paradis, E., & Claude, J. (2002). Analysis of comparative data using generalized estimating equations. *Journal of Theoretical Biology*, *218*(2), 175–185.

Paruelo, J. M., Epstein, H. E., Lauenroth, W. K., & Burke, I. C. (1997). ANPP estimates from NDVI for the central grassland region of the United States. *Ecology*, *78*(3), 953–958.

Pavoine, S., Vallet, J., Dufour, A.-B., Gachet, S., & Daniel, H. (2009). On the challenge of treating various types of variables: application for improving the measurement of functional diversity. *Oikos*, *118*(3), 391–402.

Pen, I., & Weissing, F. J. (2000). Towards a unified theory of cooperative breeding: the role of ecology and life history re-examined. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *267*(1460), 2411–2418.

Rachello-Dolmen, P. G., & Cleary, D. F. R. (2007). Relating coral species traits to environmental conditions in the Jakarta Bay/Pulau Seribu reef system, Indonesia. *Estuarine, Coastal and Shelf Science*, *73*(3–4), 816–826.

Rangel, T. F., Diniz Filho, J. A. F., & Bini, L. M. (2010). SAM: a comprehensive application for Spatial Analysis in Macroecology. *Ecography*, *33*(1), 46–50.

Ribera, I., Dolédec, S., Downie, I. S., & Foster, G. N. (2001). Effect of land disturbance and stress on species traits of ground beetle assemblages. *Ecology*, *82*(4), 1112–1129.

Savalli, U. M. (1995). The evolution of bird coloration and plumage elaboration. In Power, D. M. (Eds.), *Current Ornithology,* (141–190). Springer, Boston, MA.

Schmidt, H., & Karnieli, A. (2002). Analysis of the temporal and spatial vegetation patterns in a semi-arid environment observed by NOAA AVHRR imagery and spectral ground measurements. *International Journal of Remote Sensing*, *23*(19), 3971–3990.

Sinclair, I., Hockey, P., Tarboton, W., Hayman, P., & Arlott, N. (2002). In Sinclair, I., Hockey, P., Tarboton, Ryan, P. (Eds.), *Birds of Southern Africa*. Princeton University Press.

Somveille, M., Marshall, K. L. A., & Gluckman, T.-L. (2016). A global analysis of bird plumage patterns reveals no association between habitat and camouflage. *PeerJ*, *4*.

Stevens, M., & Merilaita, S. (2009). Defining disruptive coloration and distinguishing its functions. *Philosophical Transactions of the Royal Society B: Biological Sciences*, *364*(1516), 481–488.

Théry, M. (2001). Forest light and its influence on habitat selection. *Plant Ecology*, *153*(1/2), 251–261.

Thuiller, W., Richardson, D. M., Rouget, M., Procheş, Ş., & Wilson, J. R. U. (2006). Interaction between environment, species traits, and human uses describe patterns of plant invasions. *Ecology*, *87*(7), 1755–1769.

Vallet, J., Daniel, H., Beaujouan, V., Rozé, F., & Pavoine, S. (2010). Using biological traits to assess how urbanization filters plant species of small woodlands. *Applied Vegetation Science*, *13*(4), 412–424.

Verner, J., & Willson, M. F. (1966). The influence of habitats on mating systems of North American Passerine birds. *Ecology*, *47*(1), 143–147.

Voogd, N. J., & Cleary, D. F. R. (2007). Relating species traits to environmental variables in Indonesian coral reef sponge assemblages. *Marine and Freshwater Research*, *58*(3), 240–249.

Wilson, M. F., & von Neumann, R. A. (1972). Why are Neotropical birds more colorful than North American birds? *The Avicultural Magazine*, *78*, 141–147.

Zink, R. M., & Remsen, J. V. (1986). Evolutionary processes and patterns of geographic variation in birds. In Johnston, R. F. (Eds.), *Current Ornithology,* (1–69). Springer, Boston, MA.

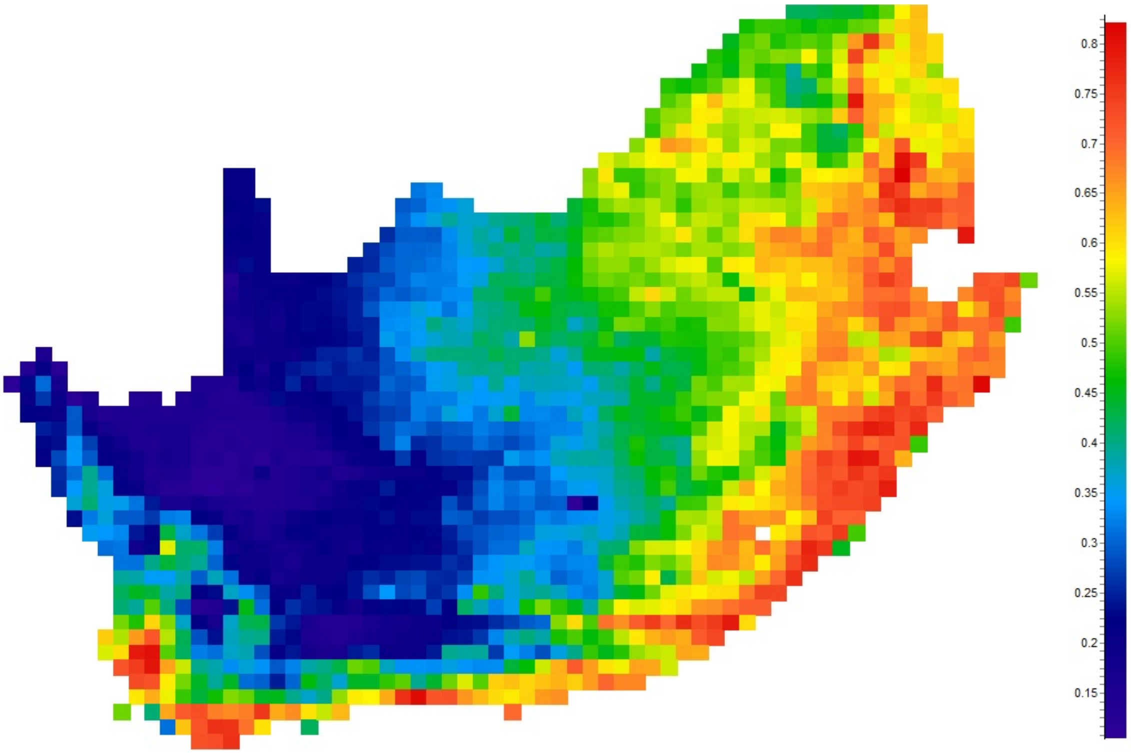


Figure 1. Geographical variation in maximum environmental productivity – average monthly maxima of NDVI values of the most productive month from the period 1982 - 2004 at the 25 × 25 km spatial resolution. Environmental productivity shows an extensive longitudinal gradient ranging from arid west to tropical east.

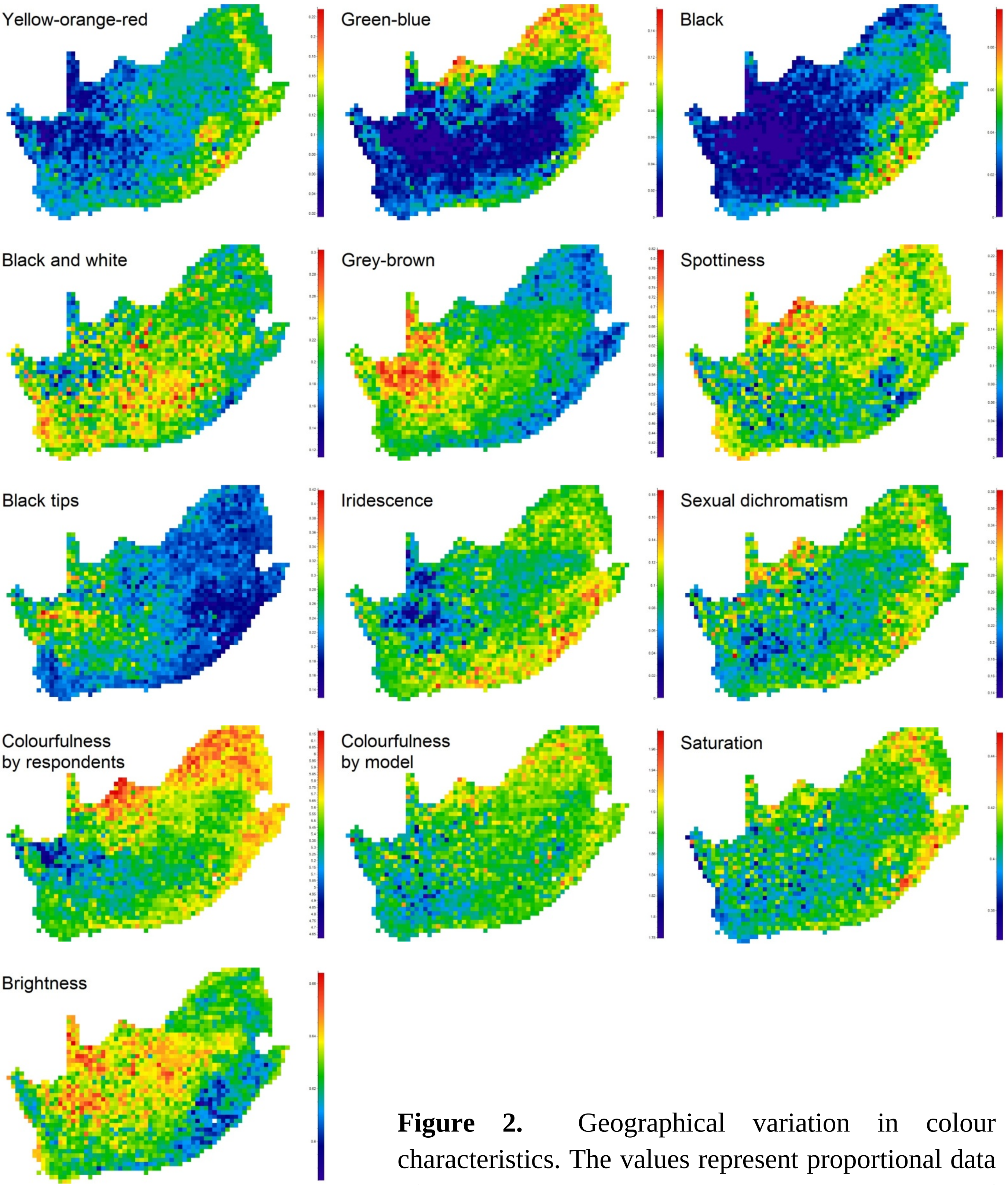


Figure 2. Geographical variation in colour characteristics. The values represent proportional data of categorical variables or the mean values of quantitative variables for species assemblages in quadrats of 25 × 25 km.

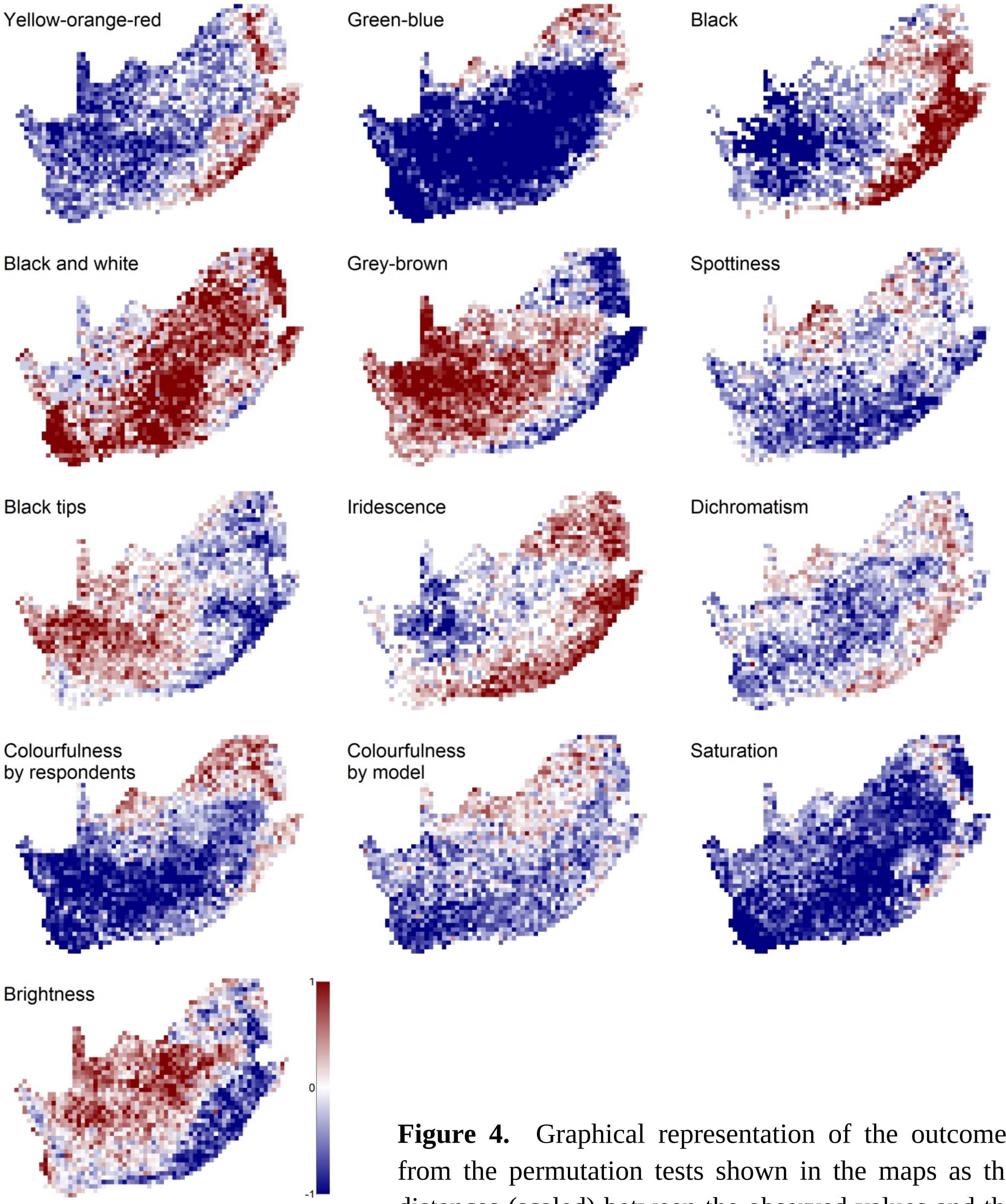


Figure 4. Graphical representation of the outcomes from the permutation tests shown in the maps as the distances (scaled) between the observed values and the theoretical values (mean trait values of randomized species assemblages) per site. By the randomization, the number of species per site was maintained, whereas the species composition of each assemblage was permuted 999 times. The denser red/blue, the more/less the species assemblages exceed in the given colour characteristic in comparison with the randomized assemblages.