

**Charles University
Faculty of Science**

Doktorský studijní program: Ekologie
Ph.D. Study Program: Ecology



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**Diverzita a životní strategie ptáků podél gradientu
produktivity a její variability**

**Bird diversity and life-history patterns along gradients of
productivity and its variation**

Disertační práce
Ph.D. Thesis

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Praha, 2019

Prohlášení:

Prohlašuji, že jsem závěrečnou práci zpracovala samostatně a že jsem uvedla všechny použité informační zdroje a literaturu. Tato práce ani její významná část nebyla předložena k získání jiného nebo stejného akademického titulu.

I declare that this thesis or any part of it was never submitted to obtain any other academic degree.

V Praze, 22. 10. 2019

Acknowledgements

First, I would like to deeply thank my supervisor David Storch for his support, advices and patience throughout all those years of my studies and work on this thesis. His guidance has brought new interesting ideas and directions in my research that fulfil and inspire me beyond my work. I greatly appreciate his valuable revision of all our manuscripts and all his overall indispensable help. I would also like to thank for our friendship.

Many thanks to my colleague David Hořák for his always positive outlook and confidence in our joint projects. I really appreciate the cooperation with David, without whom this thesis would not have been completed. I also thank my colleague Peter Mikula for his pleasant collaboration.

I would like to thank my classmates and staff of the Department of Ecology for friendly atmosphere and many great experiences. Many thanks also to the Center for Theoretical Study, where I spent a lot of time and met interesting and inspiring people who have always been very nice and I cannot imagine a better working place.

I am also very glad and thankful for having such great friends and colleagues as Irena Šímová and Eliška Bohdalková, who have been helpful in all respects, not only within work. I would like to gratefully mention also my colleague Antonín Macháček for his willingness to help and advise.

I sincerely thank my long-time friend Viki Kollerová, who has always been there for me, has given me an original look at many things, and inspired me. Thanks also to my friend Vava Vaškaninová for her positive approach and help.

Finally, I would like to express my thanks to my family, my mother and sister, for their support.

Contents

Abstract.....	1
Introduction.....	3
Chapter 1.....	23
Geographic variation in avian clutch size and nest predation risk along a productivity gradient in South Africa. Hořák, D., Sedláček, O., Tószögyová, A., Albrecht, T., Ferenc, M., Jelínek, V., & Storch, D. (2011). <i>Ostrich</i> , 82, 175–183.	
Chapter 2.....	35
Relative food limitation drives geographical clutch size variation in South African passerines: a large scale test of Ashmole's seasonality hypothesis. Hořák, D., Tószögyová, A., & Storch, D. (2015). <i>Global Ecology and Biogeography</i> , 24, 437-447.	
Chapter 3.....	61
Global diversity patterns are modulated by temporal fluctuations in primary productivity. Tószögyová, A. & Storch, D. (2019). <i>Global Ecology and Biogeography</i> .	
Chapter 4.....	81
Female solo song and duetting are associated with different territoriality in songbirds. Mikula, P., Tószögyová, A., Hořák, D., Petrusková, T., Storch, D., Albrecht, T. (2019). <i>Behavioral Ecology</i> . (accepted)	
Chapter 5.....	119
Productive environments host colourful birds: Geographical patterns in avian plumage colouration in South Africa. Tószögyová, A., Hořák, D., Kubíková, T., Storch, D. (unsubmitted manuscript)	

Abstract

Geographical variability in species richness and life-history strategies shows remarkable and well-documented patterns generated by various processes that have not yet been fully revealed. However, the pronounced correlation between spatial patterns in species and trait diversity and spatial gradients in environmental conditions indicates that the environment may modulate these processes. The mechanisms related to environmental productivity (energy availability), as a strong predictor of biodiversity, have been hypothesized to explain the cause of these broad-scale biodiversity patterns. Still, there is no consensus in the explanation, as many of the environmental and biotic factors are strongly interrelated. We have derived testable predictions that allowed disentangling the mechanisms responsible for spatial distributions of life-histories and species richness.

The patterns in spatial distribution of many avian traits across the striking productivity gradient in South Africa show a slow-fast continuum in life-history strategies. High environmental productivity in tropics may result in stable populations that favour slow life-history strategies; birds can utilize stable food resources - low food seasonality selects for small clutch sizes (Chapter 2), long parental care and high juvenile survival. The inclusion of nest predation may also contribute to the clutch size spatial trends (Chapter 1). Tropical life-histories are also indicated by the development of specific acoustic and visual signals. Cooperative breeding and the need for territory defence lead to long-term social bonds where the coordination between males and females can be represented by song in duets (Chapter 4). Strong competition for reproductive opportunities, low visibility for predators and diverse food resources in tropics can result in colourful plumage colouration (Chapter 5).

The prediction that population size-dependent extinction probability, resulting in species richness patterns, is determined by the amount of available resources, provides an interesting conception; not only the overall amount of environmental productivity, but also its temporal dynamics may drive population viability and consequently contribute to the large-scale patterns in species diversity and diversity of traits related to species persistence (Chapter 2 and 3).

Introduction

This thesis is focused on perhaps one of the most dominant patterns in ecology related to the spatial heterogeneity in different forms of biological diversity. The distribution of species richness and species life-histories across the geographical space is an interesting issue extensively studied over decades. Lately, this has been more and more possible mainly due to the availability of broad-scale data over large spatial and temporal extents and fast-growing and easily spreadable methods in their processing. The number of hypotheses that attempted to explain the cause of the geographical variability in biodiversity has also risen sharply in recent decades, but the consensus in the explanation still remains elusive; some hypotheses have been based on insufficient evidence, other controversial, or circular (Rohde, 1992; Currie, Francis, & Kerr, 1999; Willig, Kaufman, & Stevens, 2003). Another reason for competing hypotheses is that many of the species diversity predictors are correlated with latitude and each other (Hurlbert & Haskell, 2003) and are acting at different scales (Ricklefs & Schluter, 1993; Waide et al., 1999; Hurlbert & Haskell, 2003). New ideas on how to find and improve consistency in theory are therefore a major challenge.

Here I, in collaboration with co-authors, have tried to reveal the important underlying mechanisms that are responsible for large-scale patterns in the variety of life; in species traits and species richness. Thus, we have focused on the interrelated factors effects of which mask each other and often the influence of one factor was incorrectly attributed to another. We have tried to derive testable predictions that could distinguish among the roles of particular species life-histories and environmental variables in order to uncover proximate drivers of geographical variability in species features and richness. The studies, with the exception of one global study, were focused on South African avifauna, as the environment in this area, the number of bird species and the variability of their life-histories showed a prominent and extensive spatial gradient suitable for study of geographical determinants of biodiversity. Finally, we have been intensively interested in this area for many years.

Environmental and biotic determinants of life-histories spatial patterns

The variation in life-history among species across space is enormous and has attracted ecologists to explain it for decades (Lack, 1954; Partridge & Harvey, 1988; Blackburn & Gaston, 1996; Gaston & Blackburn, 1996). Life-history strategies evolve in response to the impact of various extrinsic (environmental) and intrinsic (biotic) factors on survival and reproduction (Partridge & Harvey, 1988; Stearns, 2000). There is a striking association of variation in life-history traits with

latitude and with the environmental conditions whose gradients are parallel to latitude (Martin, 2004). Therefore, environmental productivity (as well as its seasonality) represents the strongest and most ubiquitous predictor of variability in many species traits (Currie, 1991; Field et al., 2009; Williams et al., 2017). Although life-histories can show apparent correlations with environmental variables, this does not necessarily prove that the environmental variables are their proximate drivers. The environment can be a template on which certain strategies are generated followed by subsequent strategies interwoven with them (Cardillo, 2002). Thus, the environmental conditions can only indirectly affect the spatial distribution of many life-history traits. Unrevealing causality can hamper the understanding of the processes responsible for life-history diversity. In our studies (Chapter 1, 2, 4, 5), we have been interested in spatial variation in particular avian traits which have been linked with both environmental productivity and each other. Clutch size in birds is one of the essential and best-studied life-history traits. Already the pioneering studies by Moreau (1944) and Lack (1947) have shown that clutch size varies along latitude. Tropical birds tend to have smaller clutches than temperate zone birds. Nevertheless, the number of clutches per year decreases with latitude (McNamara, Barta, Wikelski, & Houston, 2008). Several hypotheses provide reasonable explanations. Food resource availability for nourishing young can be a strong determinant of clutch size, but two bodies of the food limitation concept make opposite predictions (Chapter 2). The original study by Lack (1947) claimed that clutch size reflects the total amount of food resources and thus larger clutches can be expected in productive food-rich environments. However, Ashmole (1963) later suggested that it is not the overall amount of resources, but seasonal density-dependent food influx that affects clutch size. Seasonal environments provide higher food availability for each adult during the breeding season and allow larger clutches than in average more productive environments (see below). Clutch size can also be effectively lowered by the predation pressure on nests (Skutch, 1949) which is often considered to be differential along productivity gradient (Chapter 1). Predation may also act on adults and often in conjunction with food shortages when prey is weakened by starvation (Lack, 1947). The survival probability of adults therefore decides on effort to current or future reproduction and on growth (Moreau, 1944; Martin, 2002). Nevertheless, the conclusion that there is a difference in survival between tropics and temperate is problematic (Johnston, Peach, Gregory, & White, 1997; Sandercock, Beissinger, Stoleson, Melland, & Hughes, 2000). Further studies have shown that other avian life-history traits are also associated with the productivity gradient. Tropical birds take care of their young for a longer time than temperate birds (Russell, 2000), juvenile tropical birds may therefore have slow growth rates and may mature later (Ricklefs, 1976) and prolonged parental care enhances their survival probability

compared to their temperate zone counterparts (Russell, Yom-Tov, & Geffen, 2004). In productive saturated environments, the fitness gains of the young staying in parental territories are greater than if they leave them, due to the limited supply of breeding vacancies. The higher adult survival and delayed dispersal of offspring may promote the evolution of cooperative breeding (Pen & Weissing, 2000). The rare opportunities to establish new breeding vacancies also lead to the strong selection pressure for territory defence, mate attraction and formation of long-term pairs. All these life-history traits (cooperative breeding, territoriality and stable social bonds), characteristic for stable high productive environmental conditions of tropics, may be evolutionary interwoven with signal elaboration such as female song (Chapter 4) and plumage colouration (Chapter 5). The presence of female song in duets in tropics, in contrast with female solo song occurring also in temperate regions, may then reflect the need for coordination during breeding and for effective strong defence of territories. In addition, strong competition for resources related to reproduction and breeding increases the need to visually demonstrate individual quality as a mate and/or territory competitor (Badyaev and Hill 2003). Tropical high productive environments provide sufficient resources and appropriate light conditions to express that signals of quality through colourful and conspicuous plumage.

Temporal environmental variability as a driver of biodiversity

And what governs the geographical variability in species diversity itself? As in the life-histories spatial patterns, the cause of the striking geographical pattern of unequal distribution of the species richness across the Earth has been explained by numerous hypotheses (Hutchinson, 1959; Fischer, 1960; MacArthur, 1972; Rohde, 1992; Rosenzweig, 1995; Gaston, 2000; Hawkins et al., 2003; Evans, Warren, & Gaston, 2005; Hawkins et al., 2012; Storch, Bohdalková, & Okie, 2018). They are broadly focused on history, geography, and climate as the species richness patterns are driven by the processes of speciation, colonization, and extinction. For general patterns of species diversity over broad spatial scales, the hypothesis that energy limits diversity has received probably the most attention and strong support for climatic variables associated with energy availability (Currie, 1991; O'Brien, 1993; O'Brien, 1998; Lennon, Greenwood, & Turner, 2000; Rahbek & Graves, 2001; Hawkins et al., 2003; Currie et al., 2004; Field et al., 2009; Jetz & Fine, 2012; Storch, 2012). Various mechanisms have been proposed for the species-energy theory. High temperature can accelerate speciation (Allen, Gillooly, Savage, & Brown, 2006; Allen, Gillooly, & Brown, 2007) and promote a wider range of metabolic specialists (Lovegrove, 2003; Clarke, 2003; Clarke, 2004; Anderson & Jetz, 2005; Clarke & Gaston, 2006), high environmental productivity may allow the persistence of a higher number of viable populations of different species

(Brown, 1981; Wright, 1983; Wright, Currie, & Maurer, 1993; Srivastava & Lawton, 1998; Gaston, 2000; Evans et al., 2005; Storch et al., 2018), and the climatic stability, typical for high productive tropical environments, may reduce extinction rates and/or lead to more time to adaptation leading to a higher number of coexisting species (Wiens & Donoghue, 2004; Jablonski, Roy, & Valentine, 2006; Ricklefs, 2006; Kozak & Wiens, 2012). Although the relationship between species richness and the variables of temperature, precipitation, and environmental productivity arises through different mechanisms, there is no doubt that species diversity and the processes that drive it are related to variations in contemporary climate (Hawkins, Porter, & Diniz-Filho, 2003; Hawkins et al., 2012). Especially nowadays it turns out that evidence to support history and diversification rate cannot uniformly explain the globally extensive diversity gradients (Belmaker & Jetz, 2015; Rabosky & Hurlbert, 2015; Rabosky, Title, & Huang, 2015; Oliveira et al., 2016). Whether species diversity is reached through long time for slow species accumulation or conditions for fast diversification rate (Rabosky & Hurlbert, 2015), environmental productivity, and thus the amount of resources, is a general determining factor for the number of species with viable populations that are able to persist in given environment (Gaston, 2000; Storch et al., 2018). However, the mechanisms under the species-energy relationship are complex, the amount of available resources affects population size and the variation in resources affects population dynamics. Changes in population size are not always desirable and affect the population ability to survive and persist in the environment. Therefore, the extinction probability of species depends also on the environmental fluctuations, as they affect the population fluctuations, not just on the average level of environmental conditions and the effect of mean population size itself (Ovaskainen & Meerson, 2010). The main prediction we have worked with in Chapters 2 and 3 was that temporal fluctuations in environmental productivity may contribute to the large-scale patterns in species diversity and the diversity of traits related to species persistence.

Although hypotheses based on seasonality or generally on temporal variation offered plausible explanations for some observed trends in diversity (Chesson, 2000; Cazelles et al., 2008; Hanya et al., 2011; Dalby, McGill, Fox, & Svenning, 2014), but since the influence of temporal environmental variability on species richness may be confounded with the effects of static average values of environmental variables due to their mutual collinearity, there has been only little effort to take into account temporal environmental variability into diversity predictions. Mean annual values of certain climatic variables are strong diversity predictors and the emphasis was often on finding the best predictor among them (or to compare them with other predictors) (Currie, 1991; Lennon et al., 2000; Hawkins et al., 2003) than to distinguish among particular temporal components of these variables, despite the fact that time series

data of climatic variables have been available for some decades. It would mean asking questions about another type of mechanisms generating species diversity, and temporal variation is a base of contrasting hypotheses. While the mean environmental productivity has a generally positive effect on species diversity (although the shape of the species-energy relationship depends on scale; monotonic at large scales, hump-shaped at smaller scales) (Rosenzweig, 1995; Mittelbach et al., 2001), the effect of environmental variability can be viewed from two opposite perspectives (Chesson & Huntly, 1997; Levine, Rees, & Bolker, 2004; Adler & Drake, 2008). From single-species view, environmental variability can significantly adversely affect the viability of the population and increase the risk of stochastic extinction. Moreover, from coexistence view, it can regulate the coexistence of competing species and increase diversity. The contrast between these two perspectives seems to be based on the character of temporal variability (deterministic or stochastic), on its magnitude and spatial scales.

There is a recent evidence that within-year seasonality as an important aspect of deterministic temporal variability can play a key role in generating species diversity patterns (Archibald, Bossert, Greenwood, & Farrell, 2010; Jocque, Field, Brendonck, & Meester, 2010; Dalby et al., 2014; Williams et al., 2017). The differences between species diversity in tropics and temperate regions, the latitudinal diversity gradient, are often given in relation to differentiation between stable and variable environment (Jocque et al., 2010; Dalby et al., 2014). The tropical stability in available resources, seasonal and inter-year, maintains higher diversity through the finer redistribution of the total number of individuals among species and suitable conditions for the existence of more specialists (Hutchinson, 1959; MacArthur, 1972; Jocque et al., 2010). In addition, productive tropical conditions allow formation of smaller range areas as the populations are able to pump a sufficient amount of resources from a small stable location, which leads to the higher number of populations of different species (Stevens, 1989). By contrast, increasing seasonality in environmental conditions with latitude can reduce diversity by acting as an environmental filter for certain species (Gouveia, Hortal, Cassemiro, Rangel, & Diniz-Filho, 2013), as not all species can be adapted to a wide range of different conditions or their rapid change. Moreover, seasonal environment might hamper adaptation because selection cannot continually influence organisms and they may not be able to follow periodic changes (Beissinger & Gibbs, 1993). Thus, the diversity limitations in seasonal environment are based on life-history adaptability (Varpe, 2017; Williams et al., 2017), not necessarily linked with ability for temporal variation in population size. The population may remain static over time, wherein its size is given by the lower limit in productivity variation (Hurlbert & Haskell, 2003), which reduces the number of species with viable populations even in an average

highly productive environment. However, the relatively higher seasonality in available resources compared to their minimum availability during the year leads to a relatively large increase in the amount of food resources for low population densities. Consequently, populations can respond by greater reproduction effort (Ashmole, 1963; Ricklefs, 1980) (Chapter 2) and/or higher proportion of migratory species and higher seasonal species richness (Dalby et al., 2014). Alternatively, the population can respond to seasonality through scheduled cycles in abundance (Hansson & Henttonen, 1998; Gouveia, Hortal, Cassemiro, Rangel, & Diniz-Filho, 2013; Shimadzu, Dornelas, Henderson, & Magurran, 2013; Varpe, 2017) and/or with responses to an unproductive season of the year realized through dormancy, energy storage, or seasonal migrations (Varpe, 2017).

A stronger environmental filter for species would be temporal variation in environment, if it acts stochastically (Boyce, 1992) (Chapter 3). Seasonal fluctuations in productivity may not have a harmful effect on population dynamics through unpredictable reduction in abundances, but the non-seasonal unpredictable productivity fluctuations may cause undesirable demographic stochasticity. Species in an unpredictably varying environment must behave at least in part as generalists with a set of traits enabling to cope with different conditions. Neither their adequately large ecological tolerance may not be enough, and species must react very time-flexibly, which requires another certain cognitive or migratory skills (Lytle & Poff, 2004; Varpe, 2017). Generally, organisms do not have enough ability to synchronize their life strategies/cycles with considerably unpredictable divergences from a periodic cycle in resource availability (Lytle & Poff, 2004), which inevitably leads to a decrease in species diversity. The stochastic productivity variation can cause relative rapid changes in population dynamics threatening populations to lower abundances and higher extinction risk (Boyce, 1992; Lande, 1993).

On the other hand, the coexistence theory suggests an opposite effect of temporal environmental variability on species persistence and diversity. Temporal environmental fluctuations can facilitate the coexistence of a greater number of species through preventing competitive exclusion of inferior competitors and creating niches for species in different time periods (Hutchinson, 1959; Chesson & Warner, 1981; Tilman & Pacala, 1993; Adler & Drake, 2008; Shimadzu, Dornelas, Henderson, & Magurran, 2013; Tonkin, Bogan, Bonada, Rios-Touma, & Lytle, 2017). Environmental variability gives an advantage for rare species which can store greater resource gains during unfavourable time periods than dominant species can, and so environmental variability stabilize the coexistence (Chesson, 2000; Adler, HilleRisLambers, Kyriakidis, Guan, & Levine, 2006). This storage effect allows multiple species to occupy similar habitats through sharing resources at different time (Chesson, 2000; Tonkin, Bogan, Bonada, Rios-Touma, & Lytle, 2017) (Chapter 3). In

this sense, a seasonal environment can host more specialists exploiting available temporal niches and promote higher temporal turnover in species composition (Tonkin, Bogan, Bonada, Rios-Touma, & Lytle, 2017). However, ecologists have often viewed temporal environmental variability as a detrimental factor for species richness. This is facilitated by the fact that coexistence studies are usually focused on local communities (Bogan & Lytle, 2007; Shimadzu et al., 2013) and only a few selected species (Cáceres, 1997; Adler & Drake, 2008). And by the fact that the direction of the impact of temporal environmental variability on species diversity depends on the magnitude of this variability. Species diversity increases with temporal variation in the environment as a result of temporal niche partitioning, but at some point, may decrease as the risk of stochastic extinction exceeds competitive stabilization (Letten, Ashcroft, Keith, Gollan, & Ramp, 2013; Tonkin, Bogan, Bonada, Rios-Touma, & Lytle, 2017). In addition, recent studies show that it is crucial to distinguish between a predictable seasonal and an unpredictable temporal component of environmental predictors (Tonkin, Bogan, Bonada, Rios-Touma, & Lytle, 2017) (Chapter 3), what has not been addressed in the previous studies. The importance of climate variability for stabilizing coexistence is therefore still under-explored due to the lack of appropriate large spatial scales approaches.

Main results

In Chapter 1, we have tested the prediction that clutch size is influenced by two fundamental factors; food availability and nest predation. Nest predation represents the strong selective power on the evolution of reproductive life-histories. A greater predation risk leads to lower clutch size to avoid greater losses in reproductive failure (Ricklefs, 1969). On the other hand, a high availability of food resources allows for larger clutches as adults can subsequently feed more young (Ricklefs, 1980). However, the environmental conditions may also affect predation rate, for example by the vegetation structure. Variability in environmental conditions over large spatial scales may thus influence clutch size directly through food availability and indirectly through nest predation rate. We have examined the relationship between predation rate of the artificial ground nests and clutch sizes in South African birds along the productivity gradient. Our results have shown high nest predation rate in less productive environments where lower clutch sizes are present. Although, the relationship between predation rate and clutch size of ground-nesting birds is not clear, we can assume that more productive environments with a more complex vegetation structure may reduce predator ability to find the nest. In addition, greater predator mobility in arid vegetation-sparse environments can also be responsible for this trend. However, the significant and positive relationship between environmental

productivity and clutch size indicates that food availability is the major factor affecting geographical variability in clutch size. Whether food availability for breeding adults is determined by the total amount of environmental productivity or seasonality in productivity was examined in Chapter 2.

In Chapter 4, we have studied which selective factors, represented by three life-history traits and environmental productivity, drive the female song evolution in South African songbirds. Not all female birds sing, and those who produce songs may sing with males in duets or solo. No previous studies to date have distinguished between song in duets and solo song. However, the assumed differences in functions and the apparent differences in geographical distribution between duetting song and solo song indicate that these two vocal performances were formed under different selection pressures on reproductive life-histories (Odom, Omland, & Price, 2015). We have found out that duetting is strongly associated with year-round territoriality and long-term social bonds, which is in accordance with the previous global study by Tobias et al. (2016). In addition, we have revealed that female solo song is also associated with territoriality in contrast with birds where females do not produce song. However, birds where females sing solo, defend their territories only seasonally and do not form stable social bonds so often. Cooperative breeding is not related with duetting and solo song. Even though we can assume that life-histories evolved under the impact of environmental conditions and moreover, the distribution of year-round territoriality coincides with the distribution of highly productive areas, there is no association of environmental productivity with duets and solo song. It is possible that some other unmeasured environmental variables, such as the habitat structure, drive the presence of duetting or solo song.

In Chapter 5, we have reviewed the hypothesis that birds are more colourful in tropics. Although, the previous large-scale studies (Bailey, 1978; Dalrymple et al., 2015; Friedman & Remeš, 2017) did not support this prediction, our results have been consistent with it and the environmental productivity gradient has become central to the understanding of geographical patterns in the distribution of plumage colouration in South African avifauna. More colourful species, yellow-orange-red species, green-blue species or predominantly black species occur mainly in highly productive habitats. The other end of the productivity gradient is dominated by pale grey-brown species and species with brighter feathers and with black tips of tail and wings. The spatial patterns in colouration may be explained by trade-offs between selection pressures. The prevalence of the predator-based selective pressure in arid open habitats may lead to cryptic colouration (Endler, 1978), while in tropics, it is predicted to be conspicuous for intraspecific communication or female mate choice (Badyaev & Hill, 2003). The higher availability and diversity of tropical food resources required for creation of feather pigments (Hill, 2006; McGraw, 2006), as

well as suitable light conditions of a surrounding environment may promote greater colourfulness of tropical birds (Endler, 1990). Tropical stable and rich food resources select for strong long-term territoriality, cooperative breeding and strong sexual selection (Emlen & Oring, 1977) and subsequent competition for potential mates and/or territories may promote signal elaboration such as song in duets (Chapter 4) and colourful plumage (Chapter 5).

Our studies (Chapter 2 and 3) provide strong evidence for the significant role of resources fluctuations in population persistence and generating the geographical patterns in species diversity and traits. The available resources fluctuate in time and affect the population densities and consequently the risk of population extinction (Chesson, 2000; Adler et al., 2006). Seasonal fluctuations also drive the evolution of various physiological adaptations and behaviours such as periodic growth and reproduction strategies (Williams et al., 2017). Species react by decreases in abundances in an environment with seasonal limitations in available resources and some life-history strategies reflect these low population densities during a harsh and unproductive season of the year.

In Chapter 2, we have focused on one of these life-history strategies – clutch size in birds and on the related hypothesis on food limitation proposed by Ashmole (1963). However, the original food limitation hypothesis was initially formulated by Lack (1947), who claimed that the reproductive effort of parents, measured by the number of eggs within a clutch, corresponds to the amount of food resources available for young. This original claim implies that larger clutch size should be in highly productive environments. Ashmole (1963), however, suggested that clutch size is not determined by the total amount of food resources, but by the amount relative to population density and thus to the food available to each individual. He proposed that the population densities are determined by food availability during the unproductive season of the year. Then the relatively high increase in food resources during the productive season of the year compared to their minimum availability leads to high food availability per capita and the possibility to feed more young. In this respect the stronger impact on clutch size would be represented by seasonality in food availability than its overall amount. In our study, we have decided to test Ashmole's hypothesis and distinguish between the effect of overall resource level and the effect of seasonality, which are highly correlated (Jetz, Sekercioglu, & Böhning-Gaese, 2008; Dormann et al., 2013), on clutch size in South African birds. We have confirmed the prediction that clutch size increases with seasonality when controlled for overall resource levels and decreases with maximum resource level when controlled for seasonality. Ashmole's hypothesis proved to be the most parsimonious explanation of the geographical variation in clutch size. The results were also consistent with the prediction that the number of breeding adults in

populations is regulated during the unproductive season of the year when food resources are reduced to their minimum and that the reproduction effort is dependent on the relative amount of food resources available to populations.

In Chapter 3, we provide a novel view on the importance of temporal dynamics in environmental productivity for species richness. The basic assumption was that the probability of extinction, responsible for diversity patterns, depends on population size and population fluctuations (Ovaskainen & Meerson, 2010). Both, population size and its temporal changes are affected by temporal variation in available resources (Varpe, 2017). We were interested in how the periodic and also stochastic fluctuations in environmental productivity determine spatial variability in species richness globally for three major vertebrate taxa. The contribution of our study lies in several novelties; the time-series decomposition of environmental productivity gave us a non-seasonal component that has been largely ignored. Also for the purpose to separate the influence of gradients in productivity means from temporal productivity variability, interesting relationships between them and the need for the specific approaches were revealed. We have also assumed that the temporal components of productivity variability, seasonality and unpredictability, can have very different consequences for species population dynamics, as I mentioned above. The distinguishing between these two types of fluctuations seems to be crucial in detecting specific mechanisms responsible for species diversity patterns. We have found out that temporal variation in environmental productivity significantly affects the spatial distribution of species richness. Moreover, the unpredictable productivity fluctuations can be a better species richness predictor in regions with low and high productivity levels than mean values of environmental productivity or seasonality. However, the direction of the effect of unpredictability variation is opposite in productive regions and arid unproductive regions. In productive areas, stochastic fluctuations may increase the probability of population extinction, leading to lower species richness. Whereas in arid areas, stochastic fluctuations in available resources may allow temporal niche partitioning and promote coexistence of more species. The temporal environmental variability may act as an environmental filter and at the same time as a promoter of species diversity, but depends on the mean productivity level. The findings of this study were consistent also with the results of Chapter 2. We have revealed that Ashmole's hypothesis is not applicable for granivorous birds. For granivorous species, the seed bank represents a stable food resource that controls their population dynamics. Their population densities may not decrease during the unproductive season, as they are able to gain enough food. Consequently, the benefit from the increase in food availability, mainly insects, during the productive breeding season is relatively less for granivorous species compared to other species due to the strong interspecific competition with insectivores and relatively lower food

availability for each granivore. Therefore, their clutch size is not determined by seasonality, but by the total amount of available resources. However, in this case the storage effect can be applied. The seed bank represents the stored resource of available food during the unproductive non-breeding period for granivores. The species coexistence can be facilitated through the diet specialization, when different species can benefit from different time periods when specific food resources are available.

Conclusion

Our studies have confirmed that the proximate mechanism driving geographical variation in species diversity is population size-dependent extinction dynamics modulated by environmental productivity. Although spatial variation in mean productivity is a strong predictor of species richness, spatial variation in productivity fluctuations is ubiquitous in generating species diversity patterns. In addition, our results show that temporal productivity variability may play a more important role in regulating species coexistence and persistence than comparative mean annual productivity. The results also suggest that maintaining diversity based on the storage effect may be underestimated and could provide sufficient explanation for some species richness trends at the macroecological scales.

Various global climate models predict increases in the frequency and amplitude of climate extremes such as hot days, heavy rainfall and drought (Karl & Trenberth, 2003; Salinger, 2005). It turns out that it is just these stochastic unpredictable extremes that are proving to make a significant contribution to the global patterns in biological diversity. Many studies already indicate that climate variation and climate changes may cause widespread alternations in community composition, distribution ranges, life-history strategies, interspecific interactions, and natural selection regimes (Jongejans, Kroon, Tuljapurkar, & Shea, 2010; Sorte & Jetz, 2010; Williams, Jacquemyn, Ochocki, Brys, & Miller, 2015; Siepielski et al., 2017; Kubelka et al., 2018). Therefore, it is extremely important to understand how environmental fluctuations affect biodiversity for predicting ecological consequences of the expected future increase in climate variability.

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