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Stable isotope analysis reveals variation in trophic niche depending on altitude in an endemic alpine gecko

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Abstract

Interspecific competition is considered a major determinant of ecological niche. It is hypothesized that increased competition should reduce niche breadth. However, there are scarce field tests on this hypothesis. Here, we test this central hypothesis in ecology by using the Atlas day gecko *Quedenfeldtia trachyblepharus*. This alpine gecko faces fewer competitors as altitude increases, and thereby, we predict that this species should increase niche breadth and relevant fitness parameters with altitude. We tested this prediction by analysing the isotopic signature of carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$). Our results reveal that specimens from higher altitudes showed higher values for both carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotopes, had better body condition and a greater isotopic breadth when compared to specimens from lower altitudes. Altitudinal variation in carbon values was not explained by variation in isotopic concentration in the baseline of the trophic chain. Therefore, our findings support the prediction that relaxed interspecific competition favours increased trophic niche breadth. These results also suggest that global warming may represent an important threat for this species, as it may provoke the ascent in altitude of competitors, with negative consequences for the conservation of this endemism.

Zusammenfassung

Interspezifische Konkurrenz wird als ein bedeutender Steuerungsfaktor für die ökologische Nische angesehen. Es wird angenommen, dass zunehmende Konkurrenz die Nischenbreite verringern sollte. Indessen gibt es aus dem Freiland nur wenige Überprüfungen dieser Hypothese. Hier testen wir diese zentrale Hypothese der Ökologie am Beispiel des Atlas-Taggeckos, *Quedenfeldtia trachyblepharus*. Dieser alpine Gecko ist in größeren Höhen mit weniger Konkurrenten konfrontiert, und deshalb postulieren wir, dass diese Art ihre Nischenbreite und relevante Fitnessparameter mit der Höhe steigern sollte. Wir überprüften diese Vorhersagen anhand von Analysen zu den stabilen Isotopen von Kohlenstoff ($\delta^{13}C$) und Stickstoff ($\delta^{15}N$). Individuen aus

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größeren Höhen wiesen höhere Signaturen für Kohlenstoff ($\delta^{13}C$) und Stickstoff ($\delta^{15}N$) auf, hatten eine bessere Konstitution und zeigten ein breiteres Isotopenspektrum als Individuen aus geringerer Höhe. Die mit der Höhe assoziierte Variation der C-Signaturen konnte nicht mit der Variation der Isotopenkonzentrationen an der Basis der Nahrungskette (Pflanzen) erklärt werden. Deshalb unterstützen unsere Befunde die Vorhersage, dass nachlassende interspezifische Konkurrenz eine erweiterte Nahrungsnische begünstigt. Diese Ergebnisse legen außerdem nahe, dass die globale Erwärmung eine wichtige Bedrohung für diese Art darstellen könnte, da Konkurrenten in größere Höhen aufsteigen könnten - mit negativen Folgen für den endemischen Atlas-Taggecko.

Keywords: Competition; Climate change; Carbon isotopes; Niche breadth; Nitrogen isotopes; *Quedenfeldtia trachyblepharus*

Introduction

The concept of the ecological niche is a cornerstone of Ecology (Chase & Leibold 2003). The ecological niche occupied by one species has important implications, not only for the ecology of that species, but also for the ecology of sympatric species (Schoener 1974). This is because the fundamental niche of a given species is predicted to be limited by competition with sympatric species, and species may be forced to occupy a smaller niche (the realized niche; e.g., Pianka 1974). Consequently, interspecific competition is considered a major factor determining the ecological niche breadth of sympatric species (May & MacArthur 1972). Increased competition for food, in fact, can cause a decrease in trophic niche breadth, growth rate and/or body condition (Jones & Barmuta 1998; Gómez-Mestre & Tejedo 2002; Benard & Maher 2011). Therefore, in a gradient of decreasing competition, niche breath should increase. Because of this, species inhabiting islands or alpine environments may occupy a wider trophic niche due to a lower presence of competitors (MacArthur, Diamond, & Karr 1972).

In mountain habitats there is a gradual turnover in species composition with altitude (Jankowski, Ciecka, Meyer, & Rabenold 2009). As a general pattern, species richness decreases with altitude or has a peak at middle elevations, which depends mainly on the gradient of temperature and moisture (Van Rensburg, Chown, & Gaston 2002). Those spatial changes in species composition with altitude (e.g. Fig. 1) imply changes in the number of competitors: at higher altitudes there is an ecological release in competition, and consequently, an expansion of trophic niche space is expected (Nimmo, James, Kelly, Watson, & Bennett 2011).

High mountains present harsh environmental conditions for life, as low temperatures imply reduced primary productivity, which is moreover concentrated in a small window of time. For this reason, this type of environment presents lower species richness, although it shows elevated rates of endemism (Terborgh 1977). In order to complete their life cycles, endemic alpine species display adaptations to the special environmental conditions under which they live (Arribas & Galán 2005). However, generalist species may occur in mountain communities, where they exploit these environments with lower competition, predation and, consequently, higher resource availability for a short period of time (Luiselli, Filippi, & Di Lena 2007). Nonetheless, the gradual constraints on the distributions of generalist species with altitude imply that alpine specialists have greater access to resources at high elevations, which in turn may increase population density (Díaz 1997).

In this study, we test the prediction that alpine species should increase their trophic niche breadth with altitude, as a consequence of reduced competition. We also expect that species inhabiting communities with fewer competitors will exhibit better body condition. We analysed these predictions by exploring variations with altitude in the trophic niche breadth of an endemic alpine gecko, the Atlas day gecko *Quedenfeldtia trachyblepharus*, using a stable isotope approach. It is endemic to the mountain range of the High Atlas and occurs from 1400 m altitude, reaching up to 4000 m (Bons & Geniez 1996; Schleich, Kästle, & Kabish 1996; Fig. 1); it is the only alpine gecko of the Mediterranean region. The Atlas day gecko is the dominant species in lizard communities from the alpine stage in our study area, although it becomes scarcer as altitude decreases, coinciding with an increase in the number of competitors (Fig. 1). When different species coexist, competition may result in reduced abundance, fecundity and growth (e.g., Eccard & Ylönen 2002). Therefore, if competition is higher at low altitude, we predict that this gecko's trophic niche should be narrower and that its body condition should worsen with decreasing altitude.

We investigated the trophic niche of the Atlas day gecko by using stable isotope analysis. Given that the frequency of isotopes varies throughout the trophic levels, the isotopic composition of animal tissues reflects dietary signatures of the consumed resources, as well as its position in the trophic chain (Fry 2006). This approach provides a more stable signal over time than those obtained from stomach contents or faeces (Seminoff, Jones, Eguchi, Jones, & Dutton 2006; Warne, Gilman, & Wolf 2010; Rosenblatt & Heithaus 2013). Then, stable isotope analysis became a powerful tool to overcome some of the limitations of conventional dietary studies, such as differential digestibility of prey items or their inability to reflect longer-term diet. Therefore, stable isotope analysis allows the evaluation of the trophic niche breadth of