Morphology versus realised niche: microclimatic associations of slow worms, lizards, and grass snakes

Abstract

Morphological traits are often assumed to predict ecological function, yet morphological convergence does not always imply convergence in ecological niche use. Slow worms (Anguis fragilis) are limbless lizards that superficially resemble snakes, raising the question of whether their ecological associations more closely align with lizards or snakes. This study examined realised microclimatic niche use in slow worms, lizards, and grass snakes using field-derived measurements of air temperature, average temperature, and relative humidity. Principal component analysis was used to summarise microclimatic variation, and differences among species groups were assessed using centroid comparisons, permutation-based multivariate analysis of variance, and linear modelling of the dominant microclimatic gradient. However, slow worms consistently occupied positions closer to lizards than to snakes, while snakes showed a tendency to differ along the primary microclimatic axis. Overall differentiation among species groups was weak, indicating shared use of realised environmental space. These findings suggest that limbless morphology in slow worms does not correspond to snake-like microclimatic niche use, and that behavioural and phylogenetic constraints play a more important role than external morphology in shaping ecological associations.

Introduction

Understanding how organisms interact with their environment is a central aim of ecology. For ectothermic animals, environmental conditions such as temperature and humidity strongly influence physiology, behaviour and patterns of habitat use. Consequently, variation in microclimate can shape species distributions and ecological niches, even over relatively small spatial scales. Reptiles in particular provide useful systems for examining these relationships, as their reliance on external heat sources links environmental conditions directly to activity and survival.

Reptile ecology has long emphasised the important of behavioural thermoregulation, whereby individuals actively select microhabitats that allow them to maintain favourable body temperatures and hydration status (Huey & Slatkin, 1976; Bels & Russell, 2019). Field-based studies demonstrate that reptiles often exploit fine-scale variation in microclimate through habitat choice, posture and use of refugia, rather than passively tracking ambient conditions. As a result, the environmental conditions experienced by individuals in the wild may differ substantially from broader climatic averages, highlighting the importance of microclimatic measurements in ecological analyses (Kearney et al., 2009).

Morphological traits are frequently assumed to be reliable predictors of ecological function; however, morphological convergence does not always result in ecological convergence. In squamate reptiles, similar body forms may arise through shared evolutionary history or functional adaptation without implying equivalent habitat use or environmental associations (Losos, 2011). Slow worms (*Anguis fragilis*) represent an interesting case in this context. Although taxonomically classified as lizards, slow worms are limbless and superficially resemble snakes, raising the question of whether their ecological associations more closely resemble those of lizards or snakes. Evaluating this distinction provides an opportunity to assess the extent to which morphology, phylogeny or behaviour better predicts realised ecological niche use (Vitt & Pianka, 2005).

The aim of this study was to examine whether slow worms occupy microclimatic conditions more similar to lizards or to snakes. Using field-derived measurements of temperature and relative humidity, multivariate analyses were used to compare microclimatic associations among slow worms, lizards, and grass snakes. By focusing on microclimate use rather than physiological limits, this study assesses whether limbless morphology in slow worms is associated with convergence toward snake-like ecological niche use or retention of lizard-like microclimatic associations.

Methods

The dataset analysed in this study originates from long-term reptile monitoring carried out on the island of Jersey, British Channel Islands. Surveys were conducted across a network of sites representing suitable reptile habitat within an intensively managed island landscape.

Field surveys targeted terrestrial reptile species, including slow worms (*Anguis fragilis*), lizards, and grass snakes (*Natrix natrix*), using a combination of active searching and artificial cover objects (ACOs) to enhance detection under varying environmental conditions. ACOs were positioned in thermally favourable microhabitats and were checked during standardised survey visits.

For each confirmed reptile observation, local environmental conditions were recorded at the point of encounter in order to characterise the microclimatic context of habitat use. These measurements included air temperature, substrate-associated temperatures, and relative humidity. Spatial coordinates were logged for each record, and data quality checks were applied within the original dataset to minimise duplicate detections and ensure consistency of species identification.

Detailed descriptions of survey design, site selection, and validation procedures are provided in Ward (2017), from which the present dataset is derived.

Data was organised so that only reptile observations were retained for statistical analysis, and records were filtered to include slow worms, lizards, and grass snakes. Microclimatic variables that were consistently recorded across surveys were selected for analysis, namely air temperature, average temperature and relative humidity. These climatic variables were chosen as they best represent key environmental dimensions influencing reptile activity and habitat selection (Huey & Slatkin, 1976; Bels & Russell, 2019).

To ensure comparability among variables, all microclimatic measurements were converted to numeric format and standardised prior to analysis. Records with missing values for any of the selected variables were excluded, resulting in a final dataset of 1,507 observations (slow worms: n= 908; lizards: n= 555; snakes: n= 44).

Principal component analysis (PCA) was used to summarise variation in microclimatic conditions and to visualise differences in environment among species groups. PCA was conducted on scaled air temperature, average temperature, and relative humidity variables, allowing the dominant gradients in microclimatic conditions to be identified.

The first two principal components were retained for interpretation, as together they explained the majority of variance in the dataset. Species grouping was visualised in PCA space to assess overlap and relative positioning within realised microclimatic niche space.

To test for overall differences in microclimatic space among species groups, a permutation-based multivariate analysis of variance (PERMANOVA) was conducted using Euclidean distances on PCA scores. PERMANOVA was selected as it does not assume multivariate normality and is commonly applied in ecological studies of niche differentiation.

In addition, linear models were used to assess differences among species along the primary microclimatic gradient (PC1), which explained the largest proportion of variance. All analyses were performed in R.

Results

Microclimatic analyses were conducted on a total of 1,507 observations comprising slow worms (*Anguis fragilis*, n= 908), lizards (n= 555), and grass snakes (*Natrix natrix*, n= 44). All observations included measurements of air temperature, average temperature, and relative humidity recorded during field surveys.

Principal component analysis of microclimatic variables revealed a dominant first axis (PC1) explaining 60.0% of total variance, with a second axis (PC2) explaining a further 26.5%. Together, PC1 and PC2 accounted for 86.5% of variation in microclimatic conditions. The third component explained only 13.5% of variance and was not considered further.

Visualisation of species groups in PCA space showed substantial overlap in microclimatic conditions among slow worms, lizards, and snakes (Figure 1). Despite this overlap, differences in centroid positions were evident among species groups.

Figure 1. Principal component analysis (PC1 vs PC2) of microclimatic variables (air temperature, average temperature, relative humidity) showing overlap among slow worms, lizards, and snakes, with group centroids indicated.

Mean centroid positions in PCA space differed among species groups. Slow worms occupied a centroid position closer to lizards (Euclidean distance = 0.115) than to snakes (0.377), while lizards and snakes showed the greatest separation (0.469).

Permutation-based multivariate analysis of variance detected weak overall differentiation among species groups in microclimatic space (PERMANOVA: $F_{2,1504}$ = 2.27, R^2 = 0.003, p = 0.082), indicating substantial overlap in microclimatic conditions among taxa.

Linear modelling of PC1 showed no significant difference between slow worms and lizards (estimate = -0.054, SE= 0.072, p= 0.45), whereas snakes tended to occupy lower PC1 values than lizards, with a marginal effect (estimate = -0.409, SE = 0.210, p = 0.052). Species group explained little of the total variation in PC1 (R^2 = 0.003, $F_{2,1504}$ = 1.95, p = 0.14). Differences in PC1 distributions among species groups are illustrated in Figure 2.

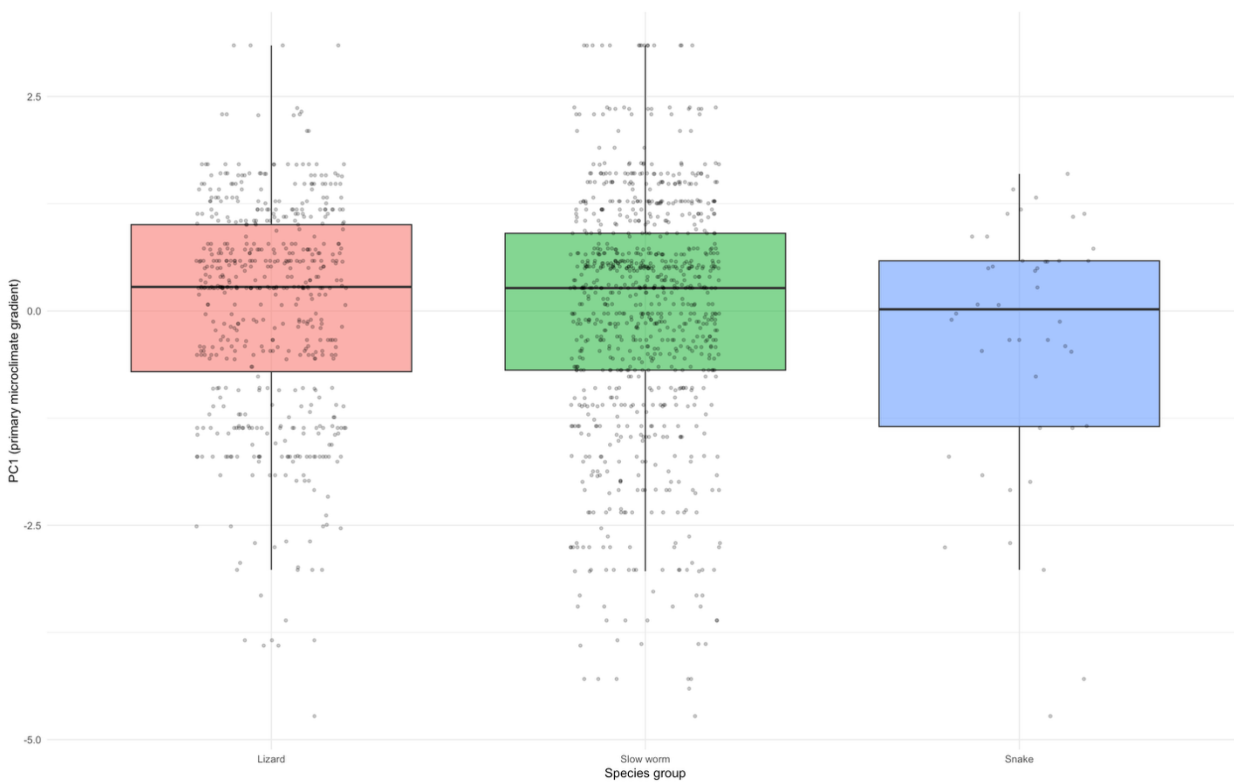

Figure 2. Distribution of PC1 scores by species group (boxplot), illustrating similarity between slow worms and lizards and a shift in snakes along the primary microclimatic gradient.

Discussion

This study examined whether slow worms (*Anguis fragilis*), despite their limbless and superficially snake-like morphology, occupy microclimatic conditions more similar to lizards or to snakes. Analyses of field-measured temperature and humidity data revealed substantial overlap in realized microclimatic space among all three groups (slow worms, lizards, snakes). However, centroid-based comparisons and univariate analysis of the primary microclimatic gradients consistently showed that slow worms were positioned closer to lizards than to snakes. These findings indicate that, at the level of realised microclimatic associations, slow worms align more closely with lizards than with snakes, suggesting that morphological convergence in body form does not necessarily translate into convergence in ecological niche use.

The observed overlap in microclimatic space among species groups is consistent with classical niche theory, which distinguishes between the fundamental niche and the realised niche of a species (Hutchinson, 1957). Because the present analysis is based on field measurements, it reflects realised microclimatic associations shaped by behaviour, habitat selection and environmental availability rather than absolute physiological limits. Under this framework, substantial overlap among taxa is expected even where morphological or physiological differences exist, as species may actively select similar subsets of available conditions in the landscape. Behavioural thermoregulation and refuge use can further constrain animals to buffered microclimates, reducing apparent ecological separation in field data (Kearney et al., 2009). Therefore, the limited differentiation observed here does not imply identical thermal physiology, but rather shared use of realised environmental space.

Although slow worms are limbless and superficially resemble snakes, their closer alignment with lizards in microclimatic space suggests that external morphology alone is a poor predictor of realised ecological function. Morphological convergence does not necessarily imply ecological convergence, as evolutionary history, behaviour, and physiological constraints can limit how species interact with their environment (Losos, 2011). In squamate reptiles, thermoregulation is strongly mediated by behaviour, including habitat choice, posture, and use of refugia, rather than body form alone (Bels & Russell, 2019). As a result, limblessness in slow worms may primarily reflect locomotor or evolutionary adaptations rather than a shift toward snake-like microclimatic niche use. This interpretation is consistent with broader patterns in reptile ecology, where phylogenetic affiliation often constrains ecological responses despite apparent morphological similarity (Vitt & Pianka, 2005).

The relative separation of snakes from both slow worms and lizards along the primary microclimatic gradient further highlights the role of behavioural ecology in shaping realised niche use. Numerous studies have shown that snakes rely heavily on specific retreat sites and refugia that provide stable thermal and hydric conditions, and that microhabitat selection in snakes is often driven by trade-offs between thermoregulation, predation risk, and shelter availability (Blouin-Demers & Weatherhead, 2002; Webb & Shine, 2009). Such reliance on discrete refugia may result in snakes experiencing a narrower or shifted range of microclimatic conditions compared to more surface-active lizards. The tendency for snakes to occupy lower PC1 values in the present analysis is therefore consistent with their documented use of buffered microhabitats rather than indicating fundamentally different physiological tolerances.

The closer alignment of slow worms with lizards in realised microclimatic space is consistent with existing evidence on the ecology of Anguis fragilis. Field studies indicate that slow worms are frequently surface-active under suitable conditions and make use of shallow refugia such as leaf litter, vegetation, and loose soil rather than deep or highly specialised retreats (Giner et al., 2024). This pattern of habitat use exposes slow worms to microclimatic conditions similar to those experienced by small lizards, despite their limbless morphology. In addition, plasticity in thermal ecology and behavioural flexibility may allow slow worms to adjust activity and habitat use in response to local conditions, further promoting overlap with lizard microclimates (Refsnider et al., 2019). Together, these factors provide a plausible ecological explanation for why slow worms occupy lizard-like realised microclimatic niches rather than converging on snake-like niche use.

This study is necessarily limited by the scope of available microclimatic variables and by imbalance in sample sizes among species groups, particularly the smaller number of snake observations. In addition, the analysis focuses on environmental conditions measured at the point of observation rather than direct measurements of body temperature or physiological performance. Nevertheless, the consistency of results across multivariate ordination, centroid comparisons, and univariate analyses suggests that the observed patterns are robust within the context of realised microclimatic niche use. Future studies incorporating body temperature data, finer-scale refuge measurements, or seasonal analyses would help to further disentangle behavioural and physiological contributions to niche differentiation. Despite these limitations, the present findings demonstrate that limbless morphology alone is insufficient to predict ecological function, and that behavioural and phylogenetic constraints play a central role in shaping microclimatic associations in squamate reptiles.

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