




The Eurasian hot nightlife: Environmental forces associated with nocturnality in lizards

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Abstract

Aim: Lizards are ancestrally diurnal, and most of them remain so. Nocturnality is common among lizards, but the environmental factors associated with lizard nocturnal activity are still unknown. Here, we contrasted the ambient temperature and productivity hypotheses, where we predicted that cold temperatures will pose a stronger limit to nocturnal species richness than diurnal lizards. Moreover, we contrasted the relative importance of annual, day and night mean temperatures to pinpoint the drivers of nocturnal lizard richness.

Location: Mainland Eurasia.

Methods: We collected distribution range and activity time data for all 1,113 lizard species found throughout mainland Eurasia. This represents the largest geographical scope to date, for studies of lizard species richness. We examined the spatial patterns of nocturnal species richness in relation to diurnal species richness across environmental gradients of ambient temperature and productivity.

Results: Nocturnal lizards are richest in the tropics and in deserts, and their richness decreases with latitude. However, nocturnal lizards are absent from the highest latitudes and coldest regions inhabited by lizards. Diurnal and nocturnal lizards respond in a similar manner to climatic factors. Ambient temperature has a strong influence on both, whereas productivity is more tightly related to the proportion of nocturnal species.

Main conclusions: Nocturnality is widespread among Eurasian lizards. However, nocturnal lizards are absent from invariably cold regions, and low temperatures seem to be a limiting factor for lizard activity period. We suggest that the year-round warm nights of the tropics reduce the cost of being active at night and open the nocturnal niche for many lizards. In hot deserts, the combination of hot days and aridity increases the cost of diurnal activity, whereas nocturnal activity provides a shelter from these extreme conditions.

KEYWORDS

ambient temperature hypothesis, night temperature, productivity hypothesis, richness

1 | INTRODUCTION

Squamates are ancestrally diurnal, and the majority of the species, genera and families have remained so. Nocturnality, however, has evolved multiple times during the evolutionary history of the group (Vitt,

Pianka, Cooper, & Schwenk, 2003). Nevertheless, as ectotherms, nocturnal lizards need to cope with both lower nighttime temperatures and a lack of external heat source.

The activity of ectotherms, such as lizards, depends primarily on external heat sources (Cowles & Bogert, 1944; Pianka & Vitt, 2003;

Viña, 2002). Also, ambient temperatures tend to have a strong influence on their body temperatures. At low body temperatures, many biochemical processes, including metabolism and assimilation of energy, slow down (e.g., Carey, Andrews, & Martin, 2003; Hemmingsen, 1960). These physiological changes, in turn, modify growth rates, reproduction, locomotion and other processes (e.g., Angilletta, Steury, & Sears, 2004; Autumn, Jindrich, DeNardo, & Mueller, 1999; Meiri et al., 2013). Thus, the environmental conditions during the night pose a challenge for lizards and other ectotherms.

Special adaptations evolved to enable lizards to maintain activity in cold temperatures. These include improved cold weather locomotion, changing diet and shifting foraging mode (e.g., Autumn et al., 1999; Bauer, 2007; Pianka & Huey, 1978; Vitt & Pianka, 2005). Among these different adaptations for maintaining the conditions for optimal functioning of cellular and organismal processes, lizards also behaviourally thermoregulate (Bartholomew, 1982; Huey, 1982). Studies of lizard nocturnality have mostly focused on thermoregulation mechanisms and not on the factors that facilitated nocturnality (e.g., Autumn, Farley, Emshwiller, & Full, 1997; Autumn, Weinstein, & Full, 1994; Hare, Gupta, Valkov, Engelman, & Cherepanov, 2010; Hitchcock & McBrayer, 2006; Huey, Niewiarowski, Kaufmann, & Herron, 1989; Kearney & Porter, 2004). Two factors that are considered as potential advantages of nocturnality are higher relative humidity during the night and avoidance of extreme high temperatures during the day (Crawford, 1934; Huey et al., 1989; Park, 1940; Puthoff, Prowse, Wilkinson, & Autumn, 2010).

Climatic conditions often predict species diversity very well (Francis & Currie, 2003). Two major climatic variables that are thought to influence species richness are ambient temperature and productivity (e.g., Brown, 2014; Buckley, Hurlbert, & Jetz, 2012; Hawkins et al., 2003; Lennon, Greenwood, & Turner, 2000; Ortiz-Yusty, Paez, & Zapata, 2013). The 'productivity hypothesis' posits that the rate of energy fixation by photosynthesis controls the diversity of plants and thus of all organisms (Wright, 1983). The 'ambient temperature hypothesis' posits that high ambient temperatures accelerate the biochemical reactions that control mutation rates and may thus increase genetic diversity, speciation rates and species richness (e.g., Allen, Brown, & Gillooly, 2002; Brown, Gillooly, Allen, Savage, & West, 2004; Rohde, 1992). The relative importance of these hypotheses is debated, and it is not clear whether they will differ between diurnal and nocturnal species.

Ambient temperature is a stronger predictor of species richness than productivity in many taxa (e.g., Brown, 2014; Lennon et al., 2000). The ambient temperature hypothesis may be especially suitable in explaining lizard richness, as their body temperature is modulated by the ambient temperature (Hawkins et al., 2003; Huey, 1982). Furthermore, because lizards have efficient water conservation mechanisms and slow metabolisms their distributions tend to be more strongly constrained by temperature than by productivity (Buckley et al., 2012; Hawkins et al., 2003; Lewin et al., 2016; Pianka & Vitt, 2003). Owing to the lack of an external heat source and its radiation, activity at night conserves water. Therefore, the distribution of nocturnal lizards is

expected to be influenced mainly by ambient temperature. Nighttime temperatures are expected to be the temperature variable most directly associated with nocturnal activity patterns. However, day temperatures might be important because nocturnal lizards may thermoregulate during the day within, or near, their retreat sites (Aguilar & Cruz, 2010; Autumn & De Nardo, 1995; Dial, 1978; Kearney & Predavec, 2000).

In order to evaluate factors driving nocturnality in lizards, we studied the relationship of nocturnal lizard richness with environmental variables. We assembled distribution maps of all lizards known to inhabit mainland Eurasia in order to: (a) assess the species richness patterns of nocturnal lizards; (b) assess the proportion of nocturnal species out of all lizards; and (c) investigate the climatic forces promoting nocturnality and test the productivity and the ambient temperature hypotheses.

2 | METHODS

2.1 | Data collection

We assembled distribution data for all 1,113 lizard species inhabiting mainland Eurasia (excluding all islands). Geographical data were assembled by members of the Global Assessment of Reptile Distributions (GARD; Roll et al., in press). Sources included the primary and grey literature, field guides and books of the lizard fauna of various regions, online meta-databases (including the IUCN; <http://www.iucn-redlist.org/>) and museum databases (including meta-databases such as GBIF, <http://www.gbif.org/>; and Vertnet, <http://vertnet.org/>). A full list of geographical data sources per species is presented in Supporting Information Appendix S1 as well as a list of the data sources. Range data were composed of three types: polygonal range maps; point locality records; and atlas data (i.e., presence in grid cells at resolutions of 0.25, 0.5 or 1.0°). Atlas data were treated as polygons with the original grid size of the source data. Point locality records were modelled to create polygons representing the extent of occurrence using hull geometries according to the work of the Global Assessment of Reptile Distribution (GARD) group (<http://www.gardinitiative.org/>).

We defined the activity time of lizard species as diurnal, nocturnal or cathemeral, based on literature data and our own observations, supplemented for 136 species by personal communication with other herpetologists (Supporting Information Appendix S1). We classified species as nocturnal when they were described as nocturnal or as nocturnal and crepuscular. Species was classified as diurnal when they were described as diurnal or as diurnal and crepuscular. Species that active at both day and night were classified as cathemeral. In our analyses, we grouped the 86 Eurasian cathemeral species (c. 7% of the species analysed) with the diurnal ones. This decision is based on the ability of cathemeral species to thermoregulate actively by basking. However, treating these species as nocturnal did not qualitatively change any of the patterns. We spatially intersected the distribution information with a Behrmann equal-area projection 1° × 1° at the equator grid cell layer (area per grid cell, 9,310 km²) to tally nocturnal, diurnal and total species richness in each grid cell. Our lizard taxonomy follows the March 2015 edition of the reptile database (Uetz, 2015).

We excluded all grid cells that contain sea area or areas that are outside the borders of our study area.

We modelled both nocturnal and diurnal species richness, as well as the proportion of nocturnal lizards out of all species, as a function of environmental variables. This was done in order to test whether ambient temperature or productivity best explains nocturnality patterns. We chose explanatory environmental variables that had the highest correlation with nocturnality proportion, from eight categories that represent different facets of ambient temperature or productivity. All variables were tested for collinearity using variance inflated factors (VIFs; Fox & Weisberg, 2011). Potential evapotranspiration (PET, as a proxy of productivity; in millimetres, 0.25° resolution; from Wilmott et al., 2001) was excluded, and the following seven variables were retained: (a) mean annual temperature (in degrees Celsius; data for variables 1–5 are at 0.16° resolution; from Hijmans, Cameron, Parra, Jones, & Jarvis, 2005); (b) diurnal range of temperature (in degrees Celsius); (c) temperature seasonality (in degrees Celsius); (d) precipitation of driest quarter (in millimetres); (e) precipitation seasonality; (f) aridity, the ratio of mean annual precipitation and mean annual PET (Barrow, 1992), which indicates the moisture availability for potential growth of reference vegetation (in millimetres, 0.008° resolution; from Trabucco & Zomer, 2009); (g) net primary productivity (NPP; in grams of carbon per year per square metre; 0.25° resolution; from Imhoff & Bounoua, 2006). Predictors 1–3 are proxies for ambient temperature, and predictors 4–7 are proxies for productivity. Despite annual temperature being the strongest temperature predictor, we also examined models that explored links to annual mean day and night temperatures (in degrees Celsius; 0.25° resolution; from the 2016 addition of NASA Earth Observations, NEO, <http://neo.sci.gsfc.nasa.gov>). In order to meet the assumptions of normal distribution and homoscedasticity, the climatic variables (except annual, day and night temperatures) were \log_{10} -transformed, and nocturnal richness proportion was logit-transformed.

The relationship between nocturnal and diurnal richness might be biome specific owing to a combination of climatic and historical factors. To test the potential influence of biome on nocturnal richness, we assigned each grid cell to the biome that occupies the largest area within it. Biomes were defined according to the 11 biomes in Eurasia (Supporting Information Appendix S2), as specified by the World Wildlife Fund (Olson et al., 2001). We excluded from the analysis biomes with < 70 grid cells, and the Boreal Forests and Taiga biomes that harbour no nocturnal lizards, and monate biomes, which are fragmented, and our distributional data prevents accurate classification of species to it. Thus, we retained four main biomes: Deserts, Mediterranean, temperate and the tropics.

2.2 | Data analysis

We tested the relationship between the seven climatic predictors and species richness and their proportion out of all lizard species in Eurasia using generalized linear models (GLMs). The best model was selected from all possible combinations based on Akaike information criterion (AIC) scores. Moran's *I* tests confirmed that there is global spatial autocorrelation in the nocturnality proportion and richness data (Moran's *I* = 0.22; $p < .001$). Therefore, we used spatial error models (SARerr) to

reduce the spatial pattern of model residuals (Dormann et al., 2007). Plotting a spatial correlogram (Supporting Information Appendix S3) depicted the pronounced effects of spatial autocorrelation at a spatial extent up to 3,000 km. We therefore defined the maximal distance in the SAR model as 3,000 km. Within multiple predictor models, we used hierarchical partitioning to assess the average contribution of each predictor to the model variance. To make the model results comparable, all the predictors' coefficients were standardized.

Differences in the climatic conditions between areas with nocturnal lizards and those that have lizards but no nocturnal species were examined using ANOVA. To test how the relationship between nocturnal and diurnal lizard richness changes across biomes we used GLMs, where nocturnal richness was the response and diurnal lizard richness and biome (as well as their interaction) were the predictors. We then used Tukey's HSD post hoc test to pinpoint the significant contrasts.

Activity patterns of Eurasian lizards are not distributed randomly throughout the suborder; there are three mainly nocturnal families (all geckos: Gekkonidae, Eublepharidae and Phyllodactylidae; see Supporting Information Appendix S4), and only three families contain a significant proportion of both diurnal and nocturnal species (Scincidae, Gekkonidae and Sphaerodactylidae). Given the strong association between nocturnality and phylogeny, there are not enough evolutionary transitions between nocturnality and diurnality to allow sufficient power for phylogenetically corrected analyses. Therefore, the possibility remains that the patterns we observe are dictated by attributes of the specific clades examined. However, we think this is not entirely the case, as the richness patterns of nocturnal species across the two main clades that contain nocturnal species (Scincidae and Gekkonidae) exhibit similar patterns across space (Supporting Information Appendix S5). Despite the relatively small number of nocturnal skinks (20 species), in both groups nocturnal species richness declines from the richest area in southeastern Asia towards northern and western Eurasia. The similarity in the patterns indicating similar environmental factors drive the richness of nocturnal species in both clades.

Spatial and statistical analyses were carried out in ArcGIS 10.0 (distributed by ESRI) and R version 3.3.0 (R Core Team, 2016). We used the 'fmsb' package (Nakazawa, 2015) for VIF analysis; the 'ape' package (Paradis et al., 2004) for Moran's *I* test; the 'pgrmss' package (Giraudoux, 2016) for spatial correlogram; the 'spdep' package (Bivand, Altman, Anselin, Assunção, & Berke, 2013) for SAR analysis; the 'MuMIn' package (Barton, 2013) for model selection; the 'relaimpo' package (Groemping, 2013) for relative importance of the predictors; the 'car' package (Fox & Weisberg, 2011) for regression analyses; and the 'multcomp' package (Hothorn et al., 2008) for Tukey's post hoc test for ANCOVA.

3 | RESULTS

Of the 1,113 lizard species that populate mainland Eurasia, 410 (37%) species are nocturnal. Five of the 12 families of lizards inhabiting this region include nocturnal species, most of them are geckos; Eublepharidae (all the 16 species), Phyllodactylidae (18 out of 27 species) and Gekkonidae (347 out of 420 species), but the families Scincidae and

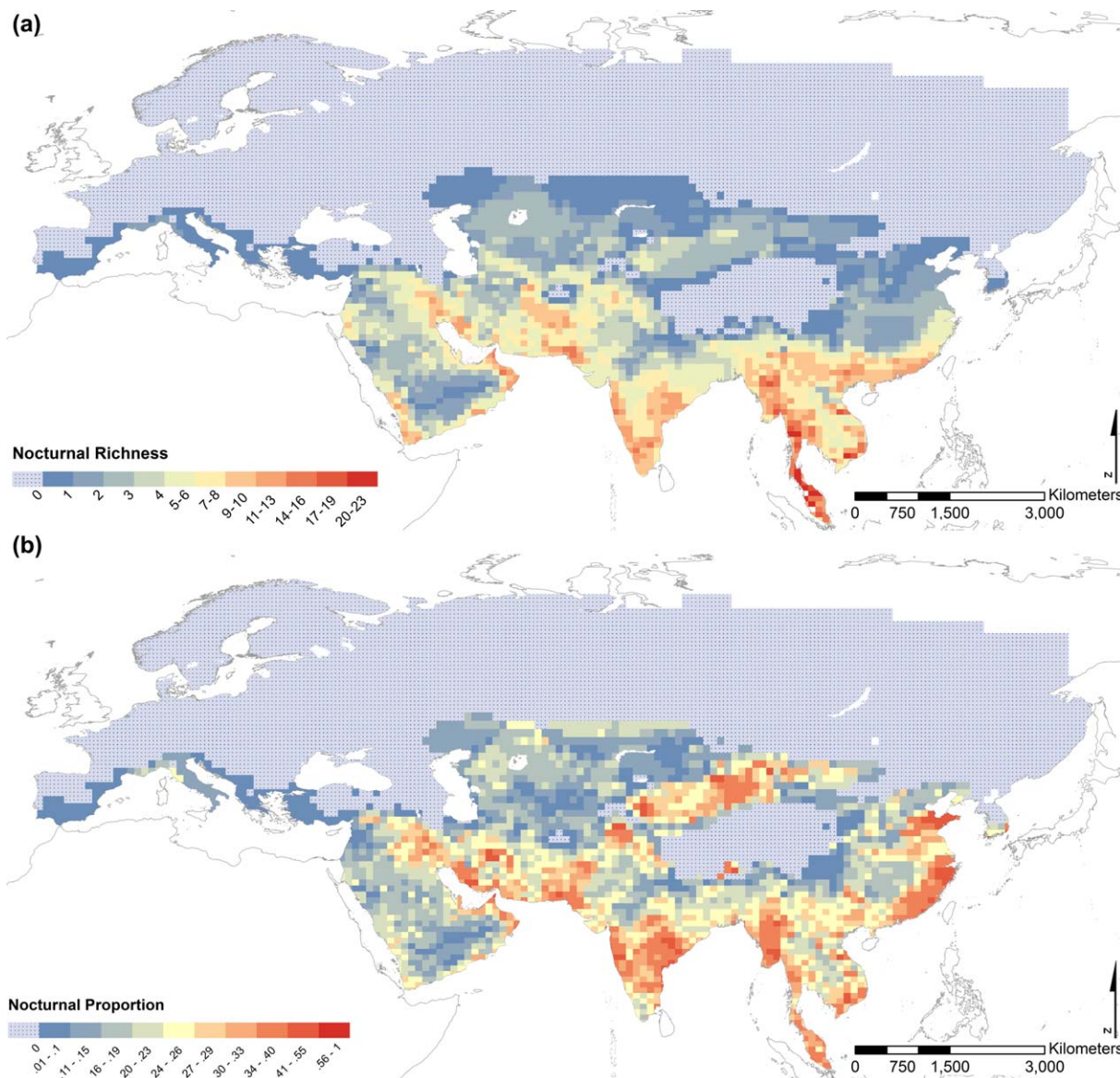


FIGURE 1 Nocturnal species richness (number of species in equal-area Behrmann projection, 9,310 km² grid cells). (a) Nocturnal lizard richness. (b) The proportion of nocturnal species out of all lizards. Hatched regions are areas that harbour only diurnal lizards

Sphaerodactylidae also include nocturnal species (Supporting Information Appendix S4).

The 4,331 cells we analysed (i.e., those inhabited by at least one lizard species, even if they contain no nocturnal species) have 1–68 lizard species in them (mean \pm SD, 12 ± 11 ; median, 8) of which 0–23 are nocturnal (2 ± 3 ; 0). The proportion of nocturnal species ranges from 0 to 0.5 (mean \pm SD, 0.10 ± 0.11 ; median, 0). Generally, both nocturnal richness and nocturnal proportion exhibit latitudinal gradients, with a decrease from the equator to the north pole (Figures 1 and 2). Nocturnal species richness declines with latitude from the richest area in southeastern Asia (especially in Malaysia, Thailand and Myanmar) towards northern Eurasia (Figure 1a). The areas richest in nocturnal species are not necessarily those with the highest proportion of nocturnal species. In fact, there are no clear geographical 'hotspots' where the proportion of nocturnal species is uniformly high (Figure 1b). Large regions harbour

only diurnal, and no nocturnal lizards; these include most of Europe (except the Mediterranean areas), the northern parts of Asia and the cold highland regions of central Eurasia (the Caucasus, Tibet and China).

The best supported spatial autoregressive (SARerr) models for nocturnal species proportion, nocturnal species richness and diurnal species richness explain 63–70% of the variances (Table 1). The models of nocturnal and diurnal richness include all the seven predictors, whereas the model of nocturnal proportion does not include temperature seasonality. For representing nocturnal richness, a model that included night temperature instead of annual temperature was better (Δ AIC = 256.6). Nocturnal species proportion and the richness of both nocturnal and diurnal species are all positively correlated with annual temperature, diurnal temperature range and aridity. Mean temperature was the strongest predictor for all the response variables. Annual temperature explains the majority (64%) of the variance in the proportion

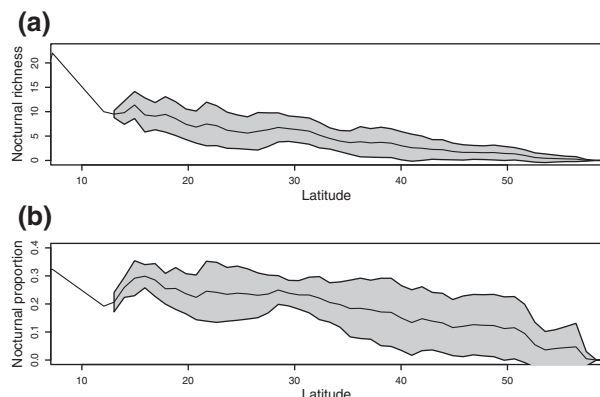


FIGURE 2 Latitudinal gradient of (a) nocturnal richness and (b) the proportion of nocturnal lizard species in Eurasia. The black lines represent the mean value across grid cells, and the grey polygons exhibit the SD. The absence of the SD polygon on the left side of the figure is attributable to the existence of only one or two analysed grid cells in the lowest latitudes

of nocturnal species. The richness of either nocturnal or diurnal species is mainly explained by the combination of mean temperature and temperature seasonality (almost 80%). The weakest predictors in all three models are NPP and temperature diurnal range (Figure 3). Overall, measures of ambient temperature predict 82% of the variances in both nocturnal and diurnal richness, whereas the productivity measures predict only 18% of these variances. In the nocturnal proportion model, the ambient temperature measures predict 67% of the variance, whereas the productivity measures predict 33% of the variance.

The relationship between nocturnal and diurnal richness is positive in all biomes, but its strength varies significantly between them (diurnal richness \times biome interaction; $F_{9,3472}=897.4$; $p \ll .0001$; Tukey's HSD; Supporting Information Appendix S6). The steepest slope is in the

tropics and the shallowest slope is in the Mediterranean and temperate biomes. The biomes also differ in intercept ($F_{5,3476}=1,509$; $p \ll .0001$); the tropics have the highest intercept, whereas the temperate biome has the lowest (Figure 4; Table 2).

Lizards inhabit almost 90% of mainland Eurasia. However, only slightly more than half of this region is occupied by nocturnal lizards. We compared the climatic conditions between areas with nocturnal lizards and those with only diurnal and cathemeral lizards. Overall, the areas with nocturnal lizards are warmer by $> 15^{\circ}\text{C}$, and their nights are $> 10^{\circ}\text{C}$ warmer than areas without nocturnal lizards. Furthermore, regions with nocturnal species have more seasonal precipitation, greater differences between diurnal and nocturnal temperatures and lower NPP, temperature seasonality and precipitation during the driest quarter. They are also less arid (Supporting Information Appendix S7; $p < .0001$ for all variables).

4 | DISCUSSION

The evolution of nocturnality in lizards seems to represent a paradox, in that the performance of lizards is enhanced by high temperatures, which they seldom experience during their nocturnal activity time (e.g., Hare, 2005; Huey, 1982; Huey & Bennett, 1987; Kearney & Predavec, 2000; Werner & Whitaker, 1978). Despite this, we found that nocturnality is fairly widespread; there are hundreds of nocturnal species, which inhabit around half of Eurasia. Overall, the proportion of nocturnal species in Eurasia (37% of the species are nocturnal) is higher than the global estimate (c. 23%; Meiri, 2016). The global figure, however, is strongly affected by the rarity of nocturnal lizards in the New World (c. 5%). The proportion of nocturnal species in Eurasia is similar to that of much of the Old World and Australia (E. Vidan & S. Meiri, unpublished data).

Neither the richness nor the proportion of nocturnal lizard species is distributed uniformly in space (Figure 1). Generally, both nocturnal

TABLE 1 Parameter estimates of the best models for nocturnal lizard proportion and richness of nocturnal and diurnal species

Response variables	Predictor	Slope (scaled)	s.e. (scaled)	p-value
Nocturnal proportion ($R^2 = .70$)	Annual temperature	0.846	0.016	$\ll .0001$
	Diurnal range	0.111	0.016	$\ll .0001$
	Aridity	0.221	0.026	$\ll .0001$
	NPP	-0.411	0.020	$\ll .0001$
	Precipitation of the driest quarter	-0.032	0.020	.0970
	Precipitation seasonality	-0.180	0.018	$\ll .0001$
Nocturnal richness ($R^2 = .68$)	Night temperature	0.637	0.016	$\ll .0001$
	Diurnal range	0.194	0.016	$\ll .0001$
	Aridity	0.361	0.026	$\ll .0001$
	NPP	-0.255	0.021	$\ll .0001$
	Precipitation of the driest quarter	-0.129	0.020	$\ll .0001$
	Precipitation seasonality	-0.169	0.018	$\ll .0001$
	Temperature seasonality	-0.311	0.018	$\ll .0001$
Diurnal richness ($R^2 = .63$)	Annual temperature	0.574	0.020	$\ll .0001$
	Diurnal range	0.272	0.017	$\ll .0001$
	Aridity	0.243	0.030	$\ll .0001$
	NPP	-0.155	0.020	$\ll .0001$
	Precipitation of the driest quarter	-0.079	0.021	.0002
	Precipitation seasonality	-0.049	0.011	$< .0001$
	Temperature seasonality	-0.321	0.015	$\ll .0001$

NPP = net primary productivity. Note. The models were chosen from all possible combination models by their highest Akaike information criterion scores.

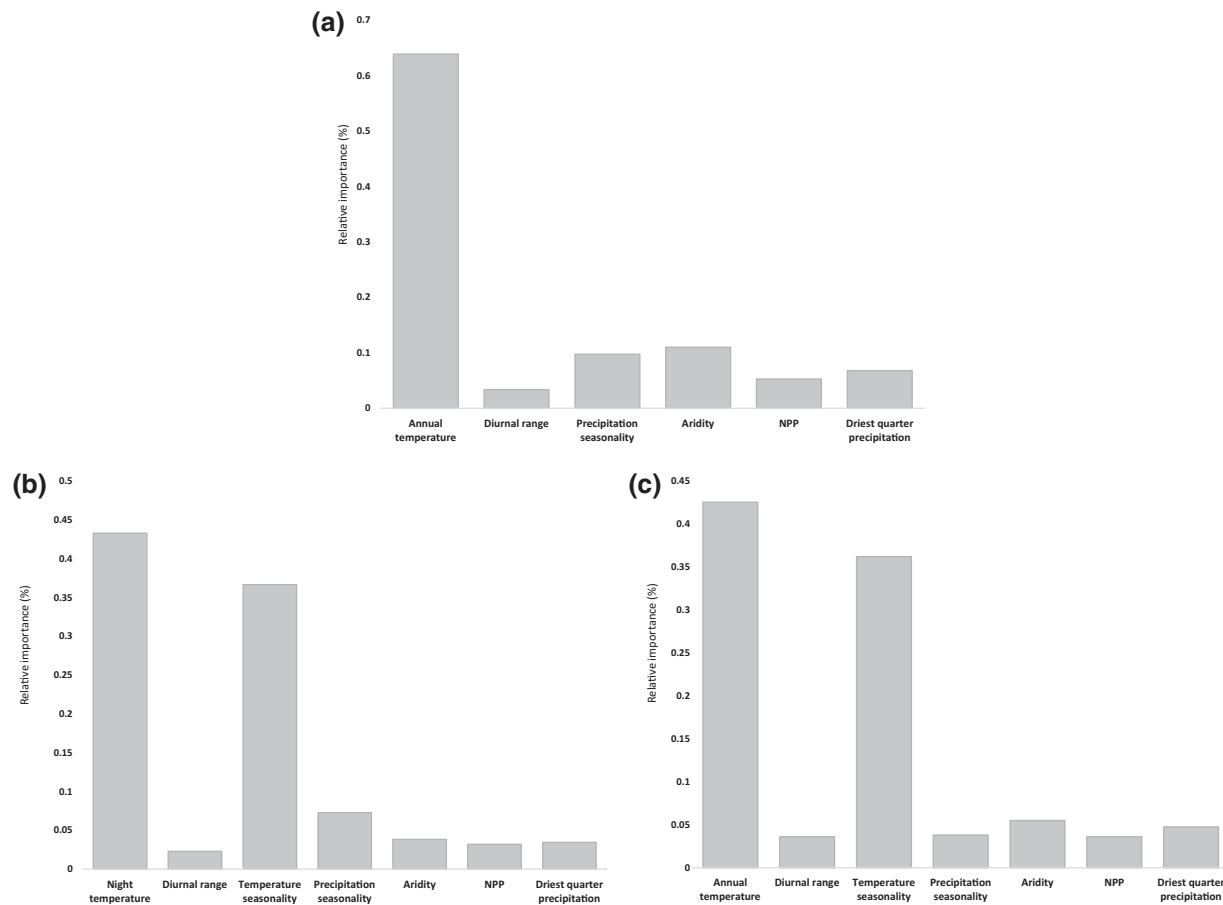


FIGURE 3 Relative importance (percentage of total variance explained) of the environmental predictors in (a) nocturnal proportion model, (b) nocturnal richness model and (c) diurnal richness model

richness and nocturnal proportion exhibit latitudinal gradients, with richness decreasing from the equator northwards (Figures 1 and 2). Although a latitudinal richness gradient is pervasive in animals, there are many exceptions (e.g., Brown 2014; Buckley, Miller, Ellison, & Gotelli, 2003; Kouki, 1999; Pyron & Burbrink, 2009; Rabenold, 1979; Willig, Kaufman, & Stevens, 2003). Some scholars have hypothesized that lizards form one of those exceptions because lizard richness is highest in hot, arid environments (Hawkins et al., 2003; James & Shine, 2000; Rabosky, Reid, Cowan, & Foulkes, 2007). This has been

supported by previous studies, which found the desert as the biome richest in lizards (e.g., Lewin et al., 2016; Powney, Grenyer, Orme, Owens, & Meiri, 2010). Nocturnal lizard richness patterns are not compatible with these results. Nocturnal lizard richness hotspots reside in the south-eastern corner of Eurasia, entirely within the tropical region. Thus, nocturnal lizard richness together with overall lizard richness patterns in Eurasia support the pervasive latitudinal diversity gradient hypothesis that puts the tropics as the richest biome for animals.

Unlike their diurnal kin, nocturnal lizards are completely absent from the highest latitudes; there are no nocturnal lizards north of latitude 57°, whereas diurnal lizards reside up to 68° N. Most of Europe, northern Asia and the highland regions of central Asia, China and Tibet are inhabited by diurnal lizards but not by nocturnal ones. These areas are cold, with low precipitation seasonality and high temperature seasonality (Supporting Information Appendix S7). These conditions mainly characterize the temperate, boreal forest and tundra biomes of the northern part of Eurasia. Low temperatures are omnipresent in all regions unoccupied by nocturnal lizards, and we suggest they are the main driver for their absence (Supporting Information Appendix S8). This has been supported by previous studies which claimed that, among all animals, reptiles are thought to have the strongest relationship with ambient temperature (Whittaker, Nogués-Bravo, & Araújo, 2007). Furthermore, previous studies demonstrated that low

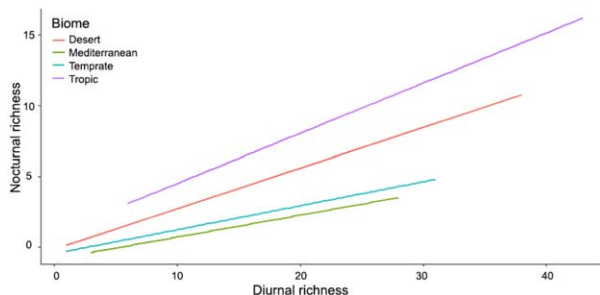


FIGURE 4 The relationship between richness of nocturnal and diurnal species per grid cell in the four main biomes of Eurasia. Each colour represents a biome

TABLE 2 Generalized linear regression of nocturnal versus diurnal species richness in the main Eurasian biomes

Biome	<i>n</i>	Percentage of cells with nocturnal sp.	Intercept \pm s.e.	Slope \pm s.e.
Deserts	1,175	91	0.07 \pm 0.002	0.29 \pm 0.01
Mediterranean	76	74	−1.06 \pm 0.137	0.16 \pm 0.05
Temperate	1,366	58	−1.17 \pm 0.046	0.17 \pm 0.01
Tropics	527	100	0.41 \pm 0.029	0.35 \pm 0.01

temperatures constrain lizard distribution and have great influence on their activity time (e.g., Buckley et al., 2010; Kearney & Porter, 2009). Interestingly, similar spatial patterns were shown in mammals (a mainly nocturnal clade). Bennie, Duffy, Inger, and Gaston (2014) found that the mammalian global activity patterns are also constrained by ambient temperature. Thus, the proportion of nocturnal species is highest in arid regions (although in lizards it is even higher in the tropics), and the diurnal proportion is higher at high altitudes in both lizards and mammals.

Annual, day and night temperatures affect nocturnality in different ways (Table 1; Figure 3). The strongest predictor of diurnal lizard richness is annual temperature, but night temperature is the strongest predictor of nocturnal lizard richness. Night temperatures are lower than daytime ones, and it is therefore unsurprising that they are a crucial factor for lizards that are active at night. Further support for the impact of low temperatures on nocturnal lizards is their absence from the colder areas. Thus, low temperatures emerge as a limiting factor on lizard activity time. Accordingly, it is surprising that day temperature does not have stronger links to diurnal lizard richness than annual temperature. High temperatures during the day should correspondingly have a greater impact on diurnal lizards. We nonetheless found that annual temperature, the predictor that averages temperatures throughout the dial cycle, is a better proxy for the spatial pattern of diurnal lizard richness (i.e., nighttime temperatures may also influence diurnal species richness).

Overall, the results of our models show that nocturnal and diurnal lizard richness respond to the same climatic variables; mainly ambient temperatures and temperature seasonality. Nocturnal proportion pattern is predominantly affected by high ambient temperatures. Our results are in line with many previous studies that found that lizard diversity is more constrained by ambient temperatures (e.g., Buckley et al., 2012; Hawkins et al., 2003; Huey, 1982; Tallowin, Allison, Algar, Kraus, & Meiri, 2017). However, the relative influence of productivity on the proportion of nocturnal lizards is not negligible. Once temperature variables are accounted for, the impact of productivity measures on nocturnality is negative. Hence, conditions of high temperatures during the day and shortage in water (as is experienced in hot deserts) might accord a relative advantage to nocturnality over diurnality. In this case, a preference for being nocturnal might evolve because high temperatures and water deficit are costly for diurnal lizards, and thus benefit the evolution of nocturnal activity in regions such as deserts. In addition, high temperatures and low temperature seasonality, which are associated with high richness of both nocturnal and diurnal lizards, are the most

characteristic of the tropics. In this biome, ambient temperature may be the only important climatic factor for lizard diversity. The unique advantages of the tropics for nocturnal lizards are the relatively high temperature during the night and the temperature stability throughout the year. These conditions reduce the cost of being active at night and enable year-round activity, so more species can use the nocturnal niche (see also Pianka, 1973). Another advantage for nocturnal lizards in the tropics and deserts might be the relative high availability of food resources (i.e., small arthropods) during the night (e.g., Erbeling & Paarmann, 1985; McNeil & Díaz, 1995; Nagy & Degen, 1988).

The spatial pattern of nocturnal species proportion is complex, with no distinct hotspots (Figure 1b). Generally, there is no noticeable pattern because diurnal and nocturnal species respond in a similar manner to the environment. However, biotic interactions, which are outside the scope of the present study, might contribute to the existence of the spatial mosaic we find. Further study should examine the additional contribution of biotic factors, such as competition (perhaps with other lizards, or with amphibians and insectivorous birds and mammals), predation (by snakes, birds and mammals) and food availability on nocturnality in lizards. These biotic interactions have been suggested not only as factors driving diversity pattern (e.g., Barrio et al., 2016; Chesson & Kuang, 2008; Michalet et al., 2006), but are also considered as possible advantages for nocturnality (i.e., weaker competition, lower predation pressures and higher food availability; e.g., Crawford, 1934; Gibbons & Semmlitsch, 1987). In addition, processes of historical (phylogenetic) biogeography may be important in the formation of nocturnality spatial pattern. The majority of nocturnal lizard species belong to the Gekkota. Thus, the nocturnality pattern is mostly determined by this lizard group. As geckos have numerous adaptations to the nocturnal environment conditions, nocturnality is assumed to have evolved early in their evolution. However, there have been multiple transitions to diurnality (Gamble, Greenbaum, Jackman, & Bauer, 2015). Further study with the combination of present-day ecological conditions and historical biogeography may deepen our understanding of nocturnality determinants.

As far as we know, this is the most wide-scale study exploring patterns of nocturnal reptile diversity. Overall, there are relatively few studies on the ecology of nocturnality. Nocturnal species are generally less studied. Nevertheless, nocturnal species may be exposed to unique anthropogenic threats, such as light pollution. Elucidating the unique ecology of nocturnal species is important in order to understand the factors facilitating nocturnality, their conservation status and particular threats. Greater focus on nocturnal species will make us more familiar with them and help us to identify their unique conservation needs.

5 | CONCLUSION

Although lizards are ancestrally diurnal, many species have adapted to nocturnal living. Opening the temporal axis of the niche foresaw the rise of hundreds of nocturnal species in different parts of Eurasia. Nocturnal lizards, like their diurnal kin, are predominantly affected by ambient temperature. However, we also show that the lowest climatic threshold for nocturnal lizards is higher than that of diurnal ones (i.e., they are precluded altogether from the highest latitudes and main highland regions where diurnal lizards can persist). This may arise from the more extreme temperatures at night, to which they are exposed. Furthermore, we highlight the tropic and desert biomes as regions with increased nocturnality of lizards. A combination of thermal and other potential drivers may have given rise to this pattern. Nevertheless, we cannot deny the influence of productivity on nocturnality, especially in hot areas. Thus, as in many other groups, richness is the highest in the most productive regions, although the mechanism leading to this pattern is still under debate (e.g., Šimová, Li, & Storch, 2013). We hope that our initial exploration of the drivers of nocturnality on a broad spatial scale and on a large database of species will pave the way to further our understanding on this seldom-explored topic.

DATA ACCESSIBILITY

The relevant data are made available with the paper.

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BIOSKETCH

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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