Biology, Ecology and Diversity

Streetlights attract a broad array of beetle species

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ABSTRACT

Light pollution on ecosystems is a growing concern, and knowledge about the effects of outdoor lighting on organisms is crucial to understand and mitigate impacts. Here we build up on a previous study to characterize the diversity of all beetles attracted to different commonly used streetlight set ups. We find that lights attract beetles from a broad taxonomic and ecological spectrum. Lights that attract a large number of insect individuals draw an equally high number of insect species. While there is some evidence for heterogeneity in the preference of beetle species to different kinds of light, all species are more attracted to some light radiating ultraviolet. The functional basis of this heterogeneity, however, is not clear. Our results highlight that control of ultraviolet radiation in public lighting is important to reduce the number and diversity of insects attracted to lights.

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Introduction

The effect of light pollution on ecosystems is a growing concern (Gaston et al., 2012; Longcore and Rich, 2004). Knowledge on how light affects the biota – and especially on organismal response to its various properties – can inform the development of environmentally friendly lighting (Gaston et al., 2012). Insects, in particular, are widely known to be attracted to lights, and knowledge on insect response to lights is generally used by collectors and in pest management (Shimoda and Honda, 2013), and it is also important in the control of vector-borne diseases (Barghini and de Medeiros, 2010). Except for a handful of species with economic or health importance, little is known about how different species respond to lights in natural ecosystems or even how this attraction affects populations (Eisenbeis, 2006; Fox, 2013). Insects are attracted to streetlights, sometimes in large numbers (Barghini and de Medeiros, 2012; Eisenbeis, 2006; Eisenbeis and Hassel, 2000), and their diversity is affected near lights even during the day (Davies et al., 2012). Street lights could have adverse effects on insect populations by a variety of mechanisms, including directly mortality caused by exhaustion or attraction of predators, or disruption of biological cycles. It is therefore important to understand what properties of street lighting cause insect attraction, and whether it affects only a few or a large array of species, in order to develop measures to minimize both the impact of lights on particular species and the number of species affected.

If compared to humans, insects have very different sensitivity spectra, usually with receptors maximally sensitive on the ultraviolet (UV), blue and green (Briscoe and Chittka, 2003). In spite of UV radiation being invisible to humans, many of the commonly used external light sources (such as high-pressure sodium vapor lamps and high-pressure mercury vapor lamps) radiate UV. These UV-radiating lamps are still widely used around the world, even though they are being steadily replaced by LED-based technologies. Several studies have shown that lamps emitting shorter wavelengths attract more insects (Barghini and de Medeiros, 2012; Eisenbeis, 2006; Eisenbeis and Hassel, 2000; Nowinszky, 2003; van Langevelde et al., 2011), and UV radiation is especially important in triggering the attraction behavior. For example, with the use of UV filters, the number of insects attracted of a blue (Hg vapor) and yellow (Na vapor) lamps are nearly indistinguishable (Barghini and de Medeiros, 2012). While it is not yet entirely clear why insects are especially attracted to UV-radiating lights, this is probably because terrestrial sources of UV interfere with insect navigation while flying (see a thorough discussion in Barghini and de Medeiros, 2010).

Most experiments on insect attraction to lights have been done in temperate environments and few have evaluated the different insect responses at the species level, without previously selecting target species to be studied, or the overall diversity of species attracted to lights. To date, this has been done mainly for moths. The abundance of moths attracted by a lamp correlates with the number of species attracted and larger moths exhibit a stronger preference for light sources radiating shorter wavelengths (Nowinszky

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et al., 2013; van Langevelde et al., 2011). In addition to size, there also seems to be differences in behavior according to taxonomy: Noctuidae moths are more attracted to shorter wavelengths, while Geometridae moths exhibit no preference (Somers-Yeates et al., 2013). Even though moths are conspicuous visitors to lights, they are not the most abundant group of insects attracted by them (Barghini and de Medeiros, 2012; Eisenbeis and Hassel, 2000; Poiani et al., 2014). It is unknown at this point if observations in moths can be generalized to other insect taxa, especially in more diverse tropical environments.

Here we study the diversity of Coleoptera, the most diverse insect order, attracted to different light sources. In a previous study, he have found that UV radiation, even in small amounts, is extremely important to trigger insect attraction to lights, but we have not studied the response of individual species (Barghini and de Medeiros, 2012). Coleoptera was one of the most abundant orders collected in our traps, and beetles represent the most species-rich order of insects, comprising over 380,000 described species (Slipiński et al., 2011), and encompassing also a wide ecological diversity (McKenna et al., 2015). To better understand the heterogeneity in insect attraction to lights in a natural setting and the diversity of insects attracted by each kind of lamp, in this study we have sorted and identified all species of Coleoptera attracted to lights in a subset of our previous sampling. We aim to understand whether commonly used street lamps that attract a larger number of individuals also attract more species in a natural setting, and also to characterize the heterogeneity in responses to lights among beetle species.

Material and methods

Collection

Here we used the material collected in the same set of experiments performed by Barghini and de Medeiros (2012), and details on the methods can be found on that paper. The test was conducted in a street surrounded by trees and isolated from urban lighting on the main campus of the University of São Paulo in the city of São Paulo. Static insect collecting traps similar to those used by Eisenbeis and Hassel (2000) were set up below lamps installed on seven-meter-tall lampposts, filled with 70% ethanol as killing agent. Each treatment utilized a full cut-off lighting fixture as follows: Hg: mercury vapor bulb protected with tempered glass; Na: high-pressure sodium vapor bulb with tempered glass; Na_F: sodium vapor bulb with tempered glass and a UV filter (Polycarbonate Lexan© 2 mm); and Control: trap without lamp. Hg is a white lamp radiating UV and shorter wavelengths. Na is a yellow lamp that radiates longer wavelengths, but also some UV. Radiation spectra for the lamps used can be found in Barghini and de Medeiros (2012).

Collections were performed in two separate campaigns. The first comprised 24 collections between March and June 2005; the second an additional 13 collections between October and December 2005. On each collection date, traps were set up before twilight and taken down in the following morning. The Coleoptera were sorted into morpho-species and identified to the family or subfamily level using various sources (Arnett et al., 2002; Arnett and Thomas, 2000; Lawrence et al., 1999). After initial identification, the classification was updated to match that used in the most recent beetle phylogeny (McKenna et al., 2015). All the material was deposited in the Museu de Zoologia da Universidade de São Paulo (MZSP).

Correlations between abundance and diversity

All statistical analyses were done in R Version 3.2.3 (R Core Team, 2015), and the data and scripts used to run the analyses and generate graphs and tables can be found in the first author's github repository (https://github.com/brunoasm/Medeiros_RBE_2016). To test whether the diversity of Coleoptera attracted to lamps is correlated with number of individuals, we used Spearman's rank correlation test considering each trap in each day as a data point. We used species richness and phylogenetic diversity (Faith, 1992) as diversity indexes, and we also tested the correlation between the two of them in the same way. To generate a phylogenetic tree to calculate phylogenetic diversity, we used the subfamily-level beetle tree from McKenna et al. (2015) as a backbone tree. Species found in this study were added by attaching a branch to a random position within the clade defined by the most recent common ancestor of the family or subfamily. Finally, species present in the backbone tree but not in this study were pruned. For the calculation of phylogenetic diversity, the age of the tree root was rescaled to 1, so that species richness and phylogenetic diversity are calculated in the same scale. We repeated the procedure to generate a total of 100 random trees to test sensitivity of the results. All manipulations used functions the R packages phytools v. 0.5-20 (Revell, 2012) and ape v. 3.4 (Paradis et al., 2004).

Effect of lamps on diversity and abundance of Coleoptera attracted

We used generalized linear mixed models to test for differences in the abundance, species richness and phylogenetic diversity of beetles collected in each treatment. In all models, the kind of lamp was considered a fixed effect and date of collection a random effect. We used a generalized linear model with Poisson error distribution and log link function for the count response variables (abundance and species richness) and a normal linear model for continuous response variables (phylogenetic diversity). In all cases, model fit was assessed graphically by generating quantile–quantile plots and predictor–residuals plots. The significance of trap as a predictor was tested with a Wald chi-square test. All calculations were done in R package lme4 v. 1.1-11 (Bates et al., 2015). To further test whether differences in diversity attracted to lights are simply a consequence of differences in abundance, we generated rarefaction curves for each lamp using functions in the R package picante v. 1.6-2 (Kembel et al., 2010).

Heterogeneity in Coleoptera preference to lights

To test for heterogeneity in the response of species to lights, we used two approaches. First, we tested whether some lamps consistently attract only a subset of beetle diversity. If that were the case, the diversity attracted to these lamps would result to be phylogenetically clustered with respect to our overall sampling. For each lamp, we calculated the mean pairwise phylogenetic distance (MPD) (Webb et al., 2002) of all species collected throughout the study, averaged over the 100 random trees. We calculated MPD both weighted and unweighted by abundance. To test whether the MPD in each lamp indicated phylogenetic clustering, we randomized the species × lamp matrix by using the trial-swap algorithm (Miklós and Podani, 2004), and drawing a new random phylogenetic tree (from the 100 trees we generated) in each replicate. We have done 10,000 replicates, with 100,000 iterations of the trial-swap algorithm per replicate. These analyses used functions in the R package picante v. 1.6-2 (Kembel et al., 2010).

We also modeled beetle behavior by using latent Dirichlet allocation (LDA) (Blei et al., 2012). The formal definitions of the model can be found in Blei et al. (2012), with a verbal explanation provided by Riddell (2014). This model is normally used in machine learning to study the distribution of topics in a collection of texts. In the traditional approach, each text document has words that are drawn from a number of topics. Each topic consists of a distribution of probabilities of usage of each word (for example, the word

'Coleoptera' has a high probability in a topic of biology and low in engineering). LDA takes as data the counts of each word in each document and, for a set number of topics, attempts to jointly infer: (1) the probability of usage of each word in each topic and (2) the probability that a randomly chosen word in a document is drawn from each topic. This model can be readily applied to our experimental set up if we consider that each species is composed of many individuals, each of which has a probability of exhibiting a given preference. Preferences are grouped into preference classes, which consist of the probabilities that an individual will be attracted to each lamp. LDA is more powerful than alternatives to characterize the preferences in our sampling because they are inferred from the whole data, including species that are common and those that are rare. The inference about each species, on the other hand, is conservative and a substantial number of specimens for a given species is needed to confidently assign it to a given preference class. In summary, we have used LDA to jointly cluster all species preferences in a minimal number of preference classes, and the probability that each species is assigned to each one of these classes. We did the inference in a Bayesian framework, using a Gibbs sampler as implemented by Griffiths and Steyvers (2004). The major adaptation needed from the document analysis context was the choice of a value for the alpha parameter. This parameter can be thought of as a control of how many specimens are needed to confidently assign a species to a behavior (or words needed to assign a document to a topic, in the original sense). Since the number of specimens per species here is much smaller than the typical number of words in a text, the traditionally used value for this parameter would be too conservative. Here we set alpha to $15/k$, where k is the number of behaviors in the model. To estimate the optimal number of preference classes for our data, we attempted to use model perplexity for a number of preference classes varying between 2 and 12. Parameters were estimated using a randomly chosen subset of 75% of the species and perplexity was calculated with the remaining 25%. After selecting the optimal number of k, we estimated model parameters using all species, running the Gibbs sampler for 1 million generations and discarding the first 100,000 generations as burn in. The chain was sampled every 100 generations and we used the sample with highest posterior probability to obtain estimates. We obtained the posterior probabilities for each lamp in the different behaviors found, as well as the taxonomy of the species that resulted to have >0.50 posterior probability of being associated with some behavior. All analyses were done using the R package topicmodels v. 0.2-3 (Grün and Hornik, 2011).

Results

We collected 1226 individuals of Coleoptera, comprising 266 species in 46 families and subfamilies (Table 1). The majority of the species resulted to be new to the collection of the MZSP. There was a large variation in the number of insects collected in different days, likely due to factors such as weather and lunar phase. Nonetheless, traps consistently collected beetles in the order Hg > Na > Na_F ≥ Control. The trend was the same for number of individuals, species richness and phylogenetic diversity (Fig. 1). Variation in the tree used to calculate phylogenetic diversity had little impact in these results. In all models, lamp type is a significant predictor, but the difference between Control and Na_F is small and not significant when taking standard errors into account (Table 2). The estimated effects were only 21% increase in abundance and 26% increase in species richness in Na_F if compared to control, but much higher for the other lights (Table 2). The use of different trees to calculate phylogenetic diversity had negligible impact on estimates and p-values, so here we present results for a randomly chosen tree. Quantile–quantile plots and analysis of residuals

Table 1
Beetles collected throughout the study. Numbers indicate number of species and (within parenthesis) number of individuals. Blank cells indicate that no individuals were collected.

| Family | Lamps | | | |
	Hg	Na	Na_F	Control
Aderidae	1 (1)	1 (1)	2 (2)	
Anthicidae	2 (2)	1 (1)		
Anthribidae				2 (2)
Archeocrypticidae	1 (1)		1 (3)	
Bostrichidae	2 (3)			2 (2)
Bothrideridae	2 (2)		1 (1)	1 (1)
Brentidae	1 (1)	1 (1)		
Cantharidae		1 (1)		
Carabidae	15 (25)	10 (19)		1 (1)
Cerambycidae	2 (2)	1 (1)	1 (1)	2 (5)
Cerylonidae			1 (1)	
Chrysomelidae	2 (2)	1 (1)	2 (2)	1 (1)
Ciidae	1 (1)			
Coccinellidae	1 (1)		1 (2)	1 (2)
Corylophidae		1 (1)	2 (2)	
Cryptophagidae	4 (43)	4 (28)	2 (24)	1 (16)
Curculionidae	2 (6)	1 (1)	3 (5)	
Curculionidae:Scolytinae	14 (41)	14 (59)	5 (11)	6 (31)
Dermestidae	1 (1)			
Dytiscidae	3 (4)			
Elateridae	1 (1)	2 (2)	2 (2)	
Endomychidae		1 (1)		
Erotylidae		2 (17)	1 (3)	
Histeridae		2 (2)		
Hybosoridae	1 (1)			
Hydrophilidae: Sphaeridiinae	5 (66)	5 (26)	2 (3)	
Laemophloeidae	5 (6)	2 (4)	1 (1)	2 (3)
Latridiidae	2 (4)	1 (18)	1 (3)	1 (5)
Leiodidae	1 (2)			
Monotomidae	3 (22)	2 (3)	1 (3)	2 (3)
Mordellidae		2 (2)		1 (1)
Mycetophagidae	1 (4)	1 (3)	1 (2)	
Nitidulidae	11 (17)	4 (8)	4 (5)	2 (2)
Phalacridae	1 (3)	2 (2)		
Ptiliidae	3 (35)	5 (29)	1 (2)	2 (2)
Ptilodactylidae	3 (3)	3 (4)	1 (3)	1 (1)
Ptinidae	3 (11)	1 (2)	1 (1)	
Ripiphoridae			1 (1)	
Scarabaeidae	7 (45)	5 (9)	1 (1)	
Scirtidae		1 (1)		
Silphidae	1 (1)			
Silvanidae	1 (5)	2 (23)	1 (4)	
Staphylinidae	62 (257)	37 (101)	14 (23)	10 (14)
Staphylinidae:Scydmaeninae	4 (6)	6 (9)	1 (1)	
Tenebrionidae	7 (8)	3 (6)		
Zopheridae	2 (2)	1 (1)		
Total	92 (38)	112 (55)	387 (126)	635 (178)

Table 2
Estimated parameters for inferred linear models, with standard errors. Significant parameters ($p < 0.05$) are highlighted in bold. Models for abundance and species richness have a log link function, so parameter estimates are multiplicative and reported in logarithmic scale. The exponential of the inferred parameters returns them to the original scale in these cases. In all models, the intercept represents counts in Control, so other parameters represent the increase in collections in relation to Control. For example, the Control treatment collected an average of $\exp(0.664) = 1.94$ insect individuals per night, while Na_F collected $\exp(0.1967) = 1.21$ times more than Control. For phylogenetic diversity, a normal linear model was used and effects are additive, not multiplicative. Wald chi-square tests compare a model with lamp type as a fixed effect with a model with only intercept, resulting in 3 degrees of freedom in all cases.

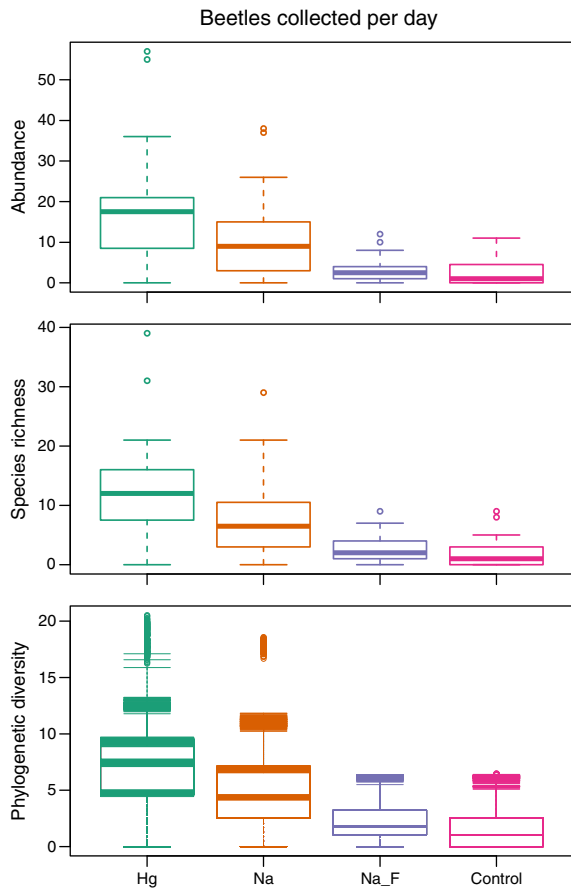|	Abundance	Species richness	Phylogenetic diversity
Intercept (control)	**0.664 ± 0.174**	**0.499 ± 0.166**	**1.54 ± 0.486**
Na_F	0.197 ± 0.149	0.231 ± 0.155	0.47 ± 0.497
Na	**1.437 ± 0.115**	**1.323 ± 0.131**	**3.51 ± 0.497**
Hg	**1.932 ± 0.111**	**1.819 ± 0.125**	**6.11 ± 0.497**
Wald chi-square	522.85 ($p < 0.001$)	352.92 ($p < 0.001$)	193.94 ($p < 0.001$)

Fig. 1. Boxplots of beetle collections in each trap (each record here is a night of collection). These are standard boxplots, with whiskers representing the more extreme values within 1.5 inter-quartile range away from each quartile. For phylogenetic diversity, we superimpose 100 boxplots obtained from different random phylogenetic trees, to highlight the sensitivity of results to phylogenetic uncertainty. Phylogenetic uncertainty has little impact on the results.

Fig. 2. Correlations between diversity and abundance across collections. Each record represents a night of collection in a given trap. Colors represent traps, with color code being the same as in Figs. 1, 3 and 4. Line represents the regression line between the two variables with intercept forced to 0.

Fig. 3. Rarefaction curves. Solid lines indicate mean and dashed lines indicate 95% confidence intervals. Inset shows the full curves for Hg and Na.

Table 3
Standardized effect size of MPD for each lamp. We show observed and randomized MPD both weighted and unweighted by abundance. p-Values for the difference are shown within parentheses.

	Weighted by abundance		Unweighted	
	Observed MPD	Mean randomized MPD	Observed MPD	Mean randomized MPD
Control	323.4	355.6 (0.001)	382.7	392.0 (0.13)
Na_F	356.3	368.8 (0.03)	383.8	393.9 (0.06)
Na	382.1	380.3 (0.67)	399.6	397.8 (0.67)
Hg	381.4	382.1 (0.38)	401.8	400.3 (0.69)

MPD, mean pairwise phylogenetic distance.

indicate a good fit for models for abundance and species richness, but not so much for phylogenetic diversity. It is likely that the normal linear model in this case could not adequately account for the excess of zero counts. It seems, however, that species richness is a good proxy for diversity in this study. In fact, both species richness (correlation 0.98, $p < 0.001$) and phylogenetic diversity (correlation 0.97, $p < 0.001$) were highly correlated with the abundance of beetles caught in each trap, as well as to each other (correlation 0.995, $p < 0.001$) (Fig. 2). In fact, rarefaction curves indicate that, controlling for the number of specimens collected, there is no significant difference between lamps Hg, Na and Na_F in the number of species captured (Fig. 3). The only exception is the Control trap, which seems to have fewer species for a given number of individuals.

There is no evidence for phylogenetic clustering in beetles attracted to lamps Hg and Na, only weak evidence for Na_F, and strong evidence for the Control trap only when the MPD is weighted by number of individuals (Table 3). We could not use perplexity as a statistic to chose an optimal number of preference classes in LDA. Perplexity decreased as the number of preference classes increased for all numbers tested. However, a close inspection of the posterior estimates showed that, for models with four or more preference classes, some of the classes were replicated, indicating overfitting. For that reason, we chose the model with only three preference classes, which was the maximum number that yielded informative results. The classes found can be described as follows: (1) individuals that are only attracted to Hg, (2) individuals that are only attracted to Na and (3) individuals that are equally attracted to Hg,
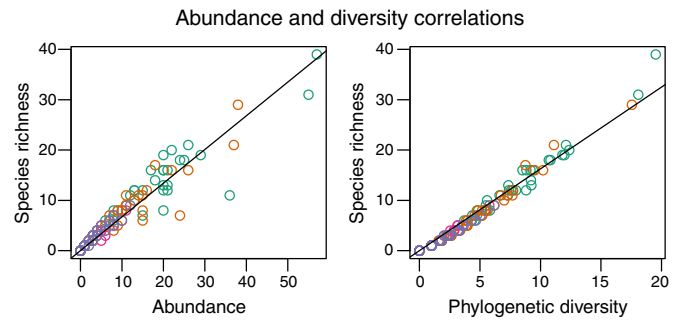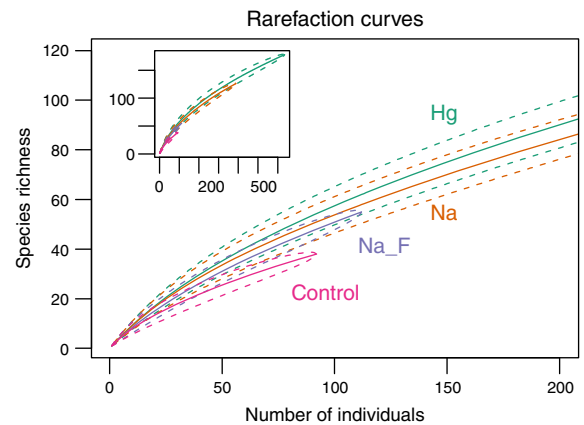
Na_F and Control. Only a few species had enough data to be assigned with >0.5 posterior probability to one of these preference classes, with the number of species and families being higher for behaviors 1 and 2 (Fig. 4).

Discussion

The first surprising finding of this study is the high diversity of beetles found in only 36 nights of collection in an urban setting. The area of study is a small fragment of secondary forest completely isolated from other fragments by the city of São Paulo. Yet, we could collect 267 species of beetles, with a little over half of them being singletons. There is no evidence for an asymptotic behavior in the rarefaction curves reported here, which suggests that the diversity of beetles potentially attracted to lights in the studied area is much higher than what we were able to sample. In spite of being attracted
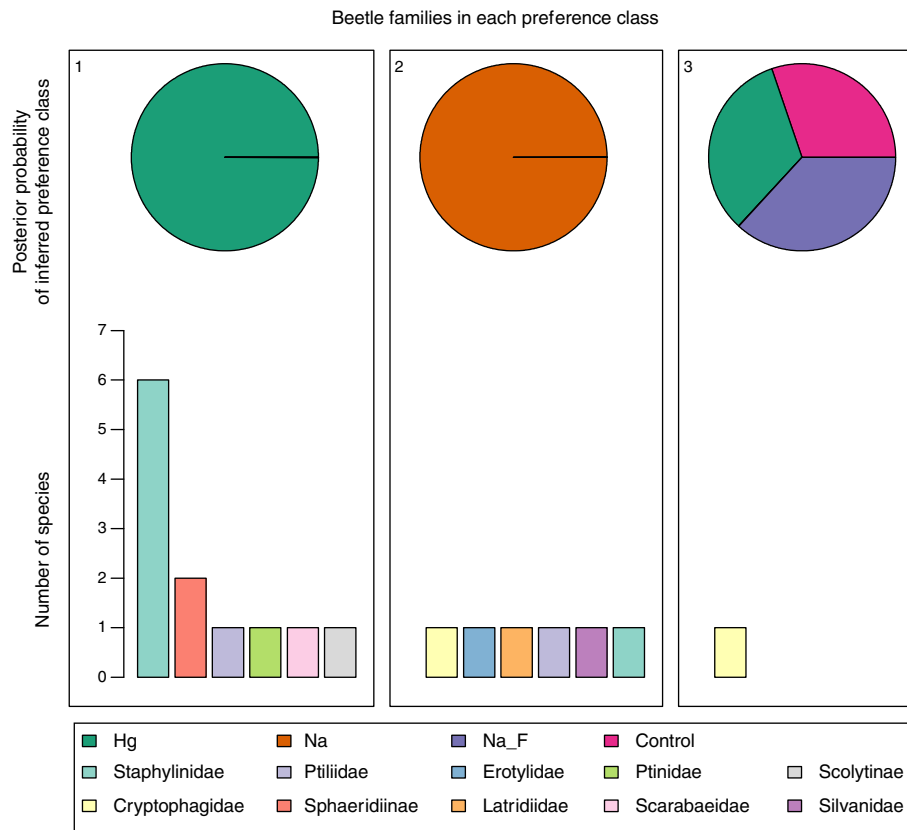
Beetle families in each preference class

Fig. 4. Preferences estimated by LDA. Boxes enclose graphs associated with preference classes estimated by LDA, numbered as 1–3. Each pie chart indicates the posterior probability of preference for each trap for a given preference class (e.g. preference class 1 includes individuals exclusively attracted to Hg). Underneath each pie chart, bars indicate the number of species with >0.5 posterior probability of being associated with the corresponding preference class, binned by higher taxon.

by lights and being found in a major city, those beetles were under-represented in the collections of MZSP, suggesting that there exists a large unexplored diversity of beetles even in areas within urban centers. Even though we did not measure specimens, it is clear that most of them represent very small beetles, ranging from 1 to 3 mm. It has been shown before that small species are less likely to be described than larger species (Stork et al., 2008), and the small size might also be the major reason why they were not collected and deposited in the MZSP before.

Beetles follow the same pattern as insects in general, in that UV-radiating lamps are more attractive and the use of a UV filter reduces collections to a level similar to the control with no light (Barghini and de Medeiros, 2012). The number of species attracted and their phylogenetic diversity also increases with number of individuals, and our results indicate that strongly attractive lamps are drawing insects from a broad taxonomic and ecological spectrum. This correlation between abundance and diversity attracted has also been found for moths (Somers-Yeates et al., 2013), indicating that it is a general pattern. It is noteworthy that the Na lamp emits only a very small fraction of its radiation in the UV range – only about 1.2% (Barghini and de Medeiros, 2012) – and yet it still attracts a significant amount of insects. The use of a UV filter in Na_F resulted in a 56% reduction in the number of species attracted and 71% in the number of individuals, highlighting the importance of controlling short-wavelength radiation in external lighting.

The use of ethanol as killing agent lured insects that are not necessarily attracted by lights. Inferred preference class 3, which consists of species attracted to almost all traps with equal probability, probably captured the dynamics of these species. In fact, the only species that was assigned to this behavior with high probability is a species of Cryptophagidae, and several less abundant species

of Scolytinae also show a trend in this direction. Both taxa are known to be attracted to ethanol (Bouget et al., 2009; Flechtmann et al., 1999). These species are also probably responsible for the phylogenetic clustering in the Control trap when species abundances are considered. In this trap, over 51% of the individuals belong to Cryptophagidae and Scolytinae (against 31% in Na_F, 22% in Na and 13% in Hg).

Species that exhibited behavior 1 (attracted to Hg) or 2 (attracted to Na) belong to multiple families, with no obvious ecological trend, but staphylinids seem to be especially attracted to mercury vapor lamps. Since there is little to no biological information available for the species collected here, it is not possible to understand the functional significance of the difference in behavior between species highly attracted to Hg and those attracted to Na. It is clear, nonetheless, that there is heterogeneity in the behavior between insect species. Preference class 2 is composed of species attracted in higher numbers to Na if compared to Hg and the other lamps, even though the Na lamp is generally less visible to insects than Hg (Barghini and de Medeiros, 2012). In Na, very little of its irradiance spectrum lies in the UV and most of it is concentrated above 550 nm, while Hg has a broader spectrum with peaks from 370 to 700 nm (Barghini and de Medeiros, 2012). Our findings contrast with results found for moths, in which individual species were consistently more attracted to a short-wavelength light source, or equally attracted to both (Somers-Yeates et al., 2013). It is possible that UV radiation, whether radiated in small or large amounts, promotes long-distance attraction in both lamps, but that some beetles avoid the bright lights of Hg once in the vicinity of the lamp. We have proposed before that this might be a mechanism for attraction of insect vectors such as kissing bugs (Barghini and de Medeiros, 2010), and our findings here are compatible with this hypothesis.

While our experimental set-up allows us to observe the heterogeneity in behaviors across a large array of species in a natural setting, a better understanding of the behavioral and physiological correlates of high attraction to different lamps would require a laboratory study using multiple species with known biology and optical sensitivity.

It is also important to highlight that LDA was unable to estimate a preference class consistent with species being more attracted to Na_F than other lamps. While 100 species were exclusively found in Hg and 47 in Na, only 17 were exclusive to Na_F, with 16 of them being singletons. This indicates that, despite some heterogeneity in the behavior of beetles, UV radiation is still the single most important factor across species. Overall, it seems that highly attractive lamps attract beetles from a broad taxonomic and ecological spectrum, with the consequence that the attraction of more individuals also results in a larger impact on diversity.

Our study adds to the growing literature on the effects of streetlights on insect communities by recording the diversity of beetles attracted to lights in a tropical environment. The use of simple UV filters in the lighting fixture of commonly used streetlights, or of new technologies that do not radiate in the UV spectrum, may reduce both the abundance and diversity of insects collected. Our results indicate that lamps that collect more insect individuals also draw from a larger diversity, even if a few species exhibit preference for lamps that are less attractive for most species. LED lights, which are gradually replacing discharge lamps in public lighting, seem to be less attractive to insects (Poiani et al., 2014), but traditionally used insect response curves do not seem to be able to predict insect attraction to lights that do not radiate a significant amount of UV (van Grunsven et al., 2014). Nonetheless, their color spectrum is more easily customizable than that of discharge lamps, so it is possible to tune LED lamps to have an adequate color temperature for humans while being less attractive to insects (Longcore et al., 2015). A future avenue for research, therefore, includes investigations on the upper limit of wavelengths highly attractive to insects, and the variation between species. If insects interpret short-wavelength visible light (such as up to 480 nm) similarly to true UV, white LED lights not carefully tuned may still have a large impact on fauna.

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgements

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