Artificial light puts ecosystem services of frugivorous bats at risk

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Summary

1. Currently, tropical forests are transformed into pasture and agricultural areas at an unprecedented rate, yet converted areas are often abandoned by farmers because depleting soil fertility renders unprofitable any agricultural land use. Natural succession of abandoned land could counter the loss of biodiversity, but the rate of natural reforestation is slow.

2. Neotropical frugivorous bats facilitate natural succession because they seem to tolerate habitat disturbance when dispersing seeds of pioneer plants. Under naturally dark conditions, bats produce a copious seed rain even in deforested habitats and connect distant forest fragments. Yet, artificial light at night may compromise bat-mediated seed dispersal if bats avoid lit areas. This may delay or jeopardize natural forest succession in fragmented tropical landscapes.

3. We asked whether the foraging behaviour of Sowell's short-tailed bats *Carollia sowelli*, a specialist on infructescences of pepper plants (Piperaceae), is negatively affected by artificial light at night.

4. First, in a dual choice experiment with captive bats, we demonstrate that food was less often explored and consumed in the dimly illuminated than in the dark compartment, indicating that artificial light alters the foraging behaviour of fruit-eating bats. Secondly, using observations in free-ranging bats, we found that infructescences were less likely to be harvested when plants were illuminated by a street lamp than under natural darkness.

5. *Synthesis and applications.* Natural succession of deforested areas and connectivity of remaining forest patches may suffer due to artificial light at night through a reduction in nocturnal seed disperser activity in lit areas. This could have negative impacts on biodiversity and consequent effects on land erosion, particularly in developing countries of the tropics where light pollution increases rapidly with growing economies and human populations. Mitigation requires that the use of artificial light should be limited in space, time and intensity to the minimum necessary. The effectiveness of 'darkness corridors' to enhance fragment connectivity and to reduce species loss should be evaluated. Policy-makers of tropical countries should become aware of the potential detrimental effects of artificial lighting on wildlife and ecosystem functioning.

Key-words: bat-facilitated succession, *Carollia sowelli*, fragmentation, frugivory, habitat connectivity, light pollution, Phyllostomidae, reforestation, seed dispersal

Introduction

Ecological light pollution, the alteration of the natural light and dark cycle by artificial light at night (Longcore & Rich 2004), has received increasing attention since it became evident that artificial light at night may be detrimental for many animals and ecosystem processes (reviewed in Rich & Longcore 2006) but continues to

spread at unprecedented rates (Hölker *et al.* 2010). Obligatorily nocturnal animals such as bats are particularly prone to night lighting, since they may be exposed to artificial light during their entire activity period. Yet, light intensities as low as moon light can potentially reduce the foraging behaviour of bats (e.g. Morrison 1978; Fleming 1988).

So far, only a few experimental studies have addressed the effects of light pollution on bats and all of those dealt with insectivorous bats mainly in the temperate zone.

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These studies have shown that some species abandon traditional commuting routes when illuminated by either high-pressure sodium (orange) or light emitting diode ('LED'; white) street lights, which potentially deterred bats from reaching their preferred foraging habitat (Stone, Jones & Harris 2009, 2012). *Eptesicus bottae* flew faster and ceased hunting insects when exposed to artificial light (Polak, Korine & Holderied 2011) and obstacle avoidance capabilities of free-ranging *Myotis lucifugus* were altered by experimental illumination (Orbach & Fenton 2010). Only a very few insectivorous species were shown to make use of insect accumulations at artificial lights (e.g. Rydell 1991) though, in these instances, their foraging effort could be reduced significantly.

In the tropics, feeding habits of bats are much more diverse than in the temperate zone. Many tropical bats consume nectar and fruits, thus offering pollination and seed dispersal services to several hundreds of plant species (Ghanem & Voigt 2012). Next to birds, frugivorous bats constitute the most numerous seed-dispersing agent in the Neotropics where they are particularly important for the dispersal of seeds during the early stages of succession (Medellin & Gaona 1999; Muscarella & Fleming 2007). Due to this important role for ecosystem functioning, bats may represent a keystone taxon in the tropics (Willig *et al.* 2007).

In contrast to insectivorous bats, fruit-eating species do not benefit from foraging at lights and therefore should preferentially stay in dark areas to avoid being visibly exposed to predators (e.g. Fleming 1988). Accordingly, indirect evidence suggests that, for example, nectar and fruit-eating lesser long-nosed bats *Leptonycteris curasoae* avoid lit areas (Lowery, Blackman & Abbate 2009). Yet, since artificial light conditions were not experimentally altered in that study, it was not possible to determine whether this effect is due to artificial light at night or to some confounding factor of urbanization, such as altered vegetation cover and/or increased noise levels. Thus far, experimental evidence for light avoidance behaviour of frugivorous bats is lacking, even though this feeding guild plays an essential role in the succession and maintenance of plant diversity especially in fragmented landscapes of the Neotropics (Muscarella & Fleming 2007). When human populations encroach in natural habitats, areas that were previously dark at night might become artificially illuminated, which may repel frugivorous bats. If these effective dispersal agents refrain from foraging in illuminated areas, artificial light at night may not only disrupt the habitats of light-sensitive species but also jeopardize the ecosystem services fruit-eating bats provide. This problem may become increasingly urgent in tropical countries with a prospering economy and an exponential growth of their human populations (CIA World Factbook 2011; UNPF state of world population 2011). Both growing economy and increased urbanization are known to correlate strongly with the degree of light pollution by street lamps (e.g. Elvidge *et al.* 2001).

We asked whether artificial light at night diminishes the harvesting activity of frugivorous bats at food plants and thus reduces the likelihood of seeds to be dispersed by bats. We focused on the effects of the widespread high-pressure sodium vapour light because high-intensity discharge lamps such as sodium lamps accounted for more than 80% of the global outdoor lighting market in 2010 (Baumgartner *et al.* 2011). Though the penetration rate of LED lights might increase, for example in Europe and North America during the forthcoming decades due to government initiatives, we believe that sodium lights will remain predominant in many developing countries of the tropics because they are cost efficient. Sodium lights have both low initial and low operating costs (Rea, Bullough & Akashi 2009), and LEDs have not yet reached a competitive cost position (Baumgartner *et al.* 2011). Further, LED street lights have been shown to repel several insectivorous bat species to a similar degree as high-pressure sodium lights (Stone, Jones & Harris 2012). To test the effect of artificial light on the harvesting activity of bats, we conducted a binary choice experiment during which we simultaneously offered fruits to Sowell's short-tailed bats *Carollia sowelli* in a dark and in a dimly illuminated compartment of a flight cage. We used Sowell's short-tailed bats because they are the primary disperser of pepper seeds (genus *Piper*), a key plant group during early succession in the Neotropics (Muscarella & Fleming 2007). We expected *C. sowelli* to evade artificial light and consequently to use the dimly illuminated compartment less often and to harvest fewer fruits from it than from the dark compartment. To ascertain the relevance of our experiment for free-living populations, we also video-recorded the feeding activity of bats at individual ripe *Piper* infructescences under dark and illuminated conditions in the wild in order to test whether the light treatment reduced the removal rate of ripe infructescences.

Materials and methods

Experiments were conducted at 'La Selva' Biological Station (Heredia Province, Costa Rica, 10°26′N, 83°59′W) in November–December 2011 and in March 2012. Monitoring of wild *Piper* plants was also conducted in November–December 2012. For both experiments, we used a custom-made street lamp to illuminate either one choice compartment or free-living *Piper* plants (see below). The lamp consisted of a high-pressure sodium light bulb ('Master SON PIA 50°W', Koninklijke Philips Electronics N.V., Eindhoven, the Netherlands) which was covered by a translucent beaker glass (Duran Group GmbH, Wertheim/Main, Germany) and operated by an electronic control gear (electronic ballast 'Ecolum EC4-70'; aplicaciones electrónicas industriales, s.l., Zaragoza, Spain). The lamp was mounted at a height of 3·5 m on a pole and powered via a wall socket. The necessary voltage of 220 V was produced by a series transformer (Voltcraft AT-400 NV; Voltcraft, Hirschau, Germany). High-intensity discharge lamps such as high-pressure sodium lamps accounted for more than 80% of the global outdoor lighting market (Baumgartner *et al.* 2011) and are commonly used as street lamps across the

world (Country Lighting Assessment). The particular light bulb used was manufactured for the use in street lamps.

CHOICE EXPERIMENT

We captured bats in a Costa Rican lowland rain forest reserve ('La Selva') by setting up 6-m and 9-m mist nets (height: 2·5 m, mesh: 16 × 16 mm; Ecotone, Gdynia, Poland) from dusk until at latest 2300 h. Bat species were identified according to Timm and LaVal (1998), and all other than adult *C. sowelli* were released immediately after capture. We transferred *C. sowelli* into a shared keeping cage (6·1 × 3·4 × 2·5 m) that was situated at a distance of about 50 m from the closest clearing and surrounded by mature forest such that bats in the keeping cage were not exposed to any artificial light but to the natural light/dark cycles. Captive bats were supplied with banana, papaya and water *ad libitum* and kept together in captivity for a maximum of 5 days before being transferred to the choice experiment.

For the choice experiment, we released individuals singly in a flight cage (Fig. 1) that was situated at a linear distance of about 250 m from the keeping cage. The experimental flight cage consisted of three compartments, the release area (5 × 3 × 2 m) and two choice compartments of equal size (2 × 1·5 × 2 m) which were separated from the release area by a retractable mesh curtain. One choice compartment was dimly illuminated by our custom-made street lamp. Since the lamp could not be dimmed sufficiently to have only low light intensities inside the choice compartment when fixing the lamp inside the choice compartment, we set up the street light outside of the flight cage at a distance of about 3 m from the rear end of the choice area (Fig. 1). Except for the front (the 'entrance'), the other choice compartment was shielded from the light by black plastic foil. To produce the same echo-acoustic environment for both choice compartments, we covered the illuminated compartment with transparent plastic foil. Between experiments, we randomly switched between illuminating the right and the left choice compartment. We set up two infrared-sensitive cameras (HDR-SR10E; Sony Corporation, Tokyo, Japan) and three infrared lights (TV6700; ABUS KG, Wetter, Germany; 24 LEDs, 2·5 W, 850 nm) to record the behaviour of bats (Fig. 1).

Depending on fruit availability, we equipped the choice compartments with ripe infructescences or fruits that local *C. sowelli* are known to forage on, namely *Piper sancti-felices, Solanum*
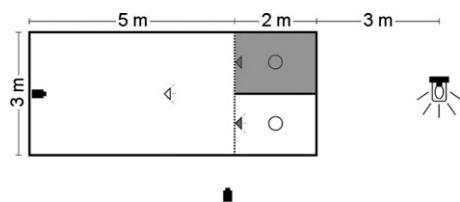
rugosum or *Ficus colubrinae*. For a given dual choice experiment, we always used same numbers of fruits of the same plant species in both compartments, in most trials this was four *Piper* infructescences. *Piper* infructescences were put with their basal part in a small plastic bowl filled with silica gel and placed centrally in the choice compartments on a platform around 80 cm in height such that bats could harvest them in flight. Branches of *Solanum* and *Ficus* with an equal number of fruits (5–15) were fixed at the ceiling of the choice compartments when we did not find enough ripe *Piper* infructescences. During some trials, we also offered banana on the central platform because we either lacked other ripe fruits or bats were not motivated to forage on fruits other than banana. Light intensity at the *Piper* infructescence was below the threshold of the luxmeter (0·01 lux; luxmeter LX-1108; Voltcraft) in the dark compartment and 4·5 ± 0·4 lux (mean ± SD) in the illuminated compartment, measured horizontally towards the lamp. This light intensity (4·5 lux) corresponds to a distance of approximately 8 m from the lamp if the light was not dimmed, assuming an isotropic light source and optimal conditions.

Experimental trials were conducted between 1830 and 0200 h. The entrance to the choice compartments was closed when we released a bat in the release area, yet the fruit scent could pass through the dividing mesh. Bats were habituated to the flight cage until they either clearly switched from flying in circles to flying back and forth in front of the choice compartments or until they stopped flying and continuously clang to the mesh for at least 30 s. We then lifted the curtain that separated the choice compartments from the release area and recorded the bat's behaviour for at least 15 min with the video cameras. After experiments, all bats were released at the site of capture.

Based on the video recordings, we counted the number of explorative flights, that is, the number of entries in each choice compartment, within 15 min after opening the choice area. To account for differences in total numbers of flights between individuals, we used a weighted regression (generalized linear model with family = binomial and link = logit) on the number of explorative flights in either choice compartment. For the regression, we incorporated the independent variables 'gender' and 'side-of-light', indicating which of the two choice compartments was illuminated, as well as the interaction between 'gender' and 'side-of-light'. The weighing was achieved in R using a two-vector object combining the number of flights in both left and right choice compartment as dependent variable for the GLM fit.

Further, we determined from the video recordings whether bats harvested fruits/infructescences in either the dark or the lit compartment. Usually, bats harvested only one infructescence and became torpid afterwards for the remaining of the recording period. In a few trials, however, bats fed on more than one fruit. For those individuals, we only included the compartment of the first feeding activity in the analysis. To evaluate whether bats harvested fruits less often under illuminated than under dark conditions, we conducted a generalized linear model for a binary response variable (family = binomial, link = logit) also incorporating 'gender', 'side-of-light' and the interaction between the two factors as predictor variables.

HARVEST OF WILD *PIPER* INFRUCTESCENCES

To verify the relevance of the flight cage experiment for free-ranging populations of bats, we also conducted a field-based light experiment. We regularly checked 14 *P. sancti-felices* plants for

Fig. 1. Scheme of the flight cage set-up. Bats could enter two choice compartments in which fruits were offered on a platform (circle). We randomly chose one of the two choice compartments to be shielded from the experimental light. We used two infrared-sensitive cameras (one in the back of the flight cage and one in line with the removable mesh (dotted line)) to observe bat behaviour. Infrared lights were installed on the ground of the release area pointing towards the choice compartments (open triangle) and one each on the ceiling of each choice compartment directed downwards (filled triangles).

ripe infructescences. Thirteen of these plants grew at the edge between secondary forest/abandoned agroforestry and the clearing (*c.* 2 ha) of the biological station (at a maximal distance of 25 m from the forest edge). One additional plant was monitored at the edge between a smaller clearing (*c.* 150 m²) and secondary forest. Plants were chosen according to the site's accessibility to electric power to run the high-pressure sodium light. However, due to numerous wall sockets at the buildings on the clearing, most *Piper* plants at the forest edge were within the range of our extension cable (*c.* 25 m), but we focused only on those that were more than 25 m apart. There is a potential lack of spatial independence in these samples due to the proximity of the *Piper* plants to each other or the identity of the foraging bats. Ideally, we would have worked on replicate study plots that are at several kilometres apart or even in different countries, but unfortunately, this approach was not feasible. Our choice of monitored plants aimed at minimizing spatial dependence given the constraints for setting up experimental lights, yet we cannot rule out the possibility that our data may suffer to some extent from a lack of independence. However, due to the high abundance of *C. sowelli* at our study site (Rex *et al.* 2008) and the overall distance of monitored *Piper* plants, we suggest that harvest events were almost independent.

At smaller plants, we were able to mark every ripe infructescence when monitoring the respective plant since *Piper* plants produce only a few ripe infructescences each night over extended periods of time. At large plants with many ripe infructescences, we randomly chose a subset of the ripe ones. Every *Piper* plant was used at least twice, once under naturally dark conditions and once when it was illuminated by the experimental street light. At most plants, however, we increased the number of infructescences monitored by marking ripe infructescences on more than one dark and one illuminated night ($n = 63$ marked infructescences for dark and light condition, respectively). On average, we marked 5 ± 4 and 5 ± 3 (mean $\pm$ SD) infructescences per plant during dark and illuminated conditions, respectively (min to max = 1–14 and 1–10), shortly before sunset by knotting a short piece (*c.* 5 cm) of thin orange thread to the branch at a distance of about 5 cm from the respective ripe infructescence. Due to the orange colour of the sodium vapour light, the thread was only distinguishable from the plant by its colour during daylight but not during dark or artificially lit conditions. Three hours following sunset, we counted the number of marked infructescences that were harvested.

The light was placed at a mean ($\pm$SD) distance of 2.5 ± 0.7 m from the observed infructescences. It was switched on before sunset and ran until midnight. The mean light intensity ($\pm$SD) was 57.0 ± 19.1 lux at the monitored *Piper* infructescences under illuminated conditions which is comparable to light intensities measured underneath or in proximity to high-pressure sodium street lights (e.g. Stone, Jones & Harris 2009: 52 lux). During the dark treatment, light intensity was below the threshold of the luxmeter (0·01 lux). Light intensities were measured horizontally at a height of 1·8 m towards the lamp using the luxmeter LX-1108 (Voltcraft). The nature of the first treatment (either dark or light) was assigned randomly to experimental plants. After each illuminated monitoring, we waited at least three nights before using the same plant again under dark conditions to avoid any sequential effects on the outcome of the experiments.

We used a logistic regression framework to analyse the influence of light on the probability of fruits to be harvested by bats.
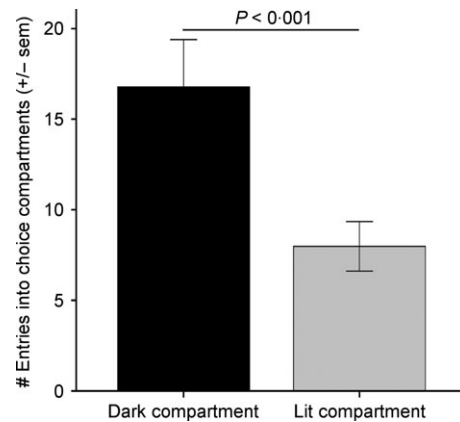

Fig. 2. Observed mean number of entries per bat from 56 *Carollia sowelli* bats in either the dark or the dimly illuminated ('lit') choice compartment.

The dependent variable y of the model was a binary variable, indicating whether a given fruit had been harvested ($y = 1$) or not ($y = 0$). We considered the light treatment as a binary variable (defined by: $0 =$ dark, $1 =$ light) modelled as a fixed effect, and we modelled the plant identity as a random effect to account for the lack of independence of fruits marked at the same bush. As such, the model corresponds to a generalized linear mixed effect model (GLMM) that we fitted using the function 'glmer' from the packages LME4 v. 0.999999-2 (Bates, Maechler & Bolker 2013). We tested the effect of the light treatment by comparing the observed likelihood ratio test statistic measured for this covariate to its distribution under the null hypothesis obtained by parametric bootstrap (referred as PBtest in the results). This was done using the function 'PBmodcomp' from the package PBKR-TEST v.0.3-5 (Halekoh & Højsgaard 2013) that we used through the wrapper package AFEX v. 0.5-71 (Singmann 2013).

At a subset of 12 plants, we also video-recorded a randomly chosen ripe infructescence under both dark and illuminated conditions from sunset until midnight. From those recordings, we determined the time (minutes after sunset) at which the respective infructescence was harvested. We then tested for significant differences between the two treatments using the paired-samples *t*-test in PASW statistics 18.0 (SPSS Inc., Chicago, IL, USA).

If not mentioned otherwise, all analyses were conducted in R (R Core Team 2012). We used an alpha value of 5%.

Results

In our dual choice experiment, we conducted 56 experimental trials using 39 male and 17 female *C. sowelli*. The number of explorative flights in either choice compartment was affected by light treatment ($Z = 8.87$, $P < 0.001$) but not by gender ($Z = -0.84$, $P = 0.402$) nor by the interaction between gender and light treatment ($Z = 0.94$, $P = 0.349$). Bats performed less explorative flights in the dimly illuminated than in the dark compartment (Fig. 2). On average, bats entered the dimly illuminated compartment four times (median; min/max = 0 and 41, respectively) and the dark compartment eight times (median; 0–88). The light treatment also affected in which

compartment bats harvested food ($Z = -2.29$, $P = 0.022$), but neither gender ($Z = -0.48$, $P = 0.35$) nor the interaction between gender and light treatment ($Z = 1.16$, $P = 0.247$) had an effect on this decision. Bats harvested food almost twice as often in the dark than in the dimly illuminated compartment ($N_{dark} = 36$, $N_{light} = 20$).

In the free-ranging population, our camera recordings ($N = 40$) revealed that after sunset no other vertebrates besides bats harvested infructescences of *P. sancti-felices* at our study site.

We found that the light treatment exerted a significant influence on the probability of a fruit being harvested (PBtest: likelihood ratio test statistics = 19.2, 666 simulations reaching convergence, $P < 0.009$, Fig. 3a). In the naturally dark environment, 100% ($N = 63$) of fruits were harvested within 3 h after sunset, while the model predicts that only 89.5% of fruits were harvested on each plant under illumination. This estimate deviates slightly from the 77.8% (49 of 63) of infructescences that were harvested across all plants during the experiment because the removal rates differed between plants (variance of the random effect expressed in the logit scale = 4.77) and the data collection was not balanced with respect to plants, while model estimates are.
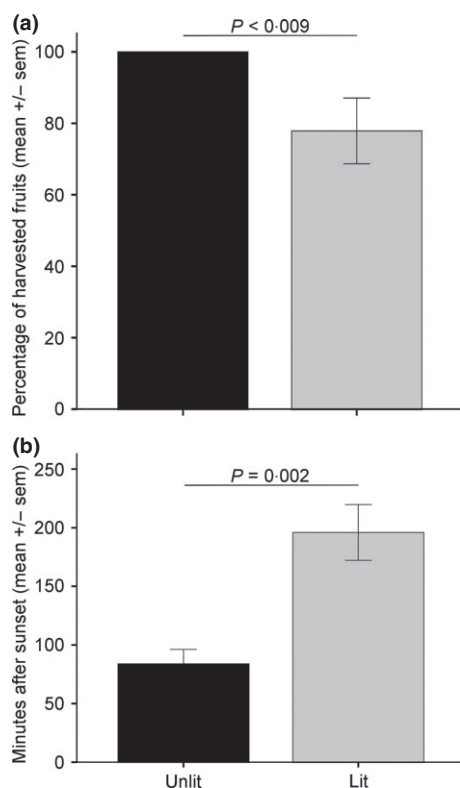

Fig. 3. (a) Observed percentage of harvested *Piper sancti-felices* infructescences among all marked ones ($n = 14$ plants) and (b) for infructescences that were harvested, the minutes after sunset when infructescences were harvested by free-ranging bats from plants in either a naturally dark surrounding ('unlit') or from the same plants under illumination of a street lamp ($n = 12$ infructescences each from a different *P. sancti-felices* plant for dark and illuminated conditions, respectively).

If harvested at all, infructescences under illumination were harvested about 2 h later than infructescences from the same plants but in a dark surrounding (mean $\pm$ SD = 84 $\pm$ 42 min and 196 $\pm$ 82 min after sunset, respectively; paired-samples $T = -4.1$, $N = 12$, $P = 0.002$; Fig. 3b).

Discussion

Our study provides first evidence that frugivorous bats are repelled by artificial light at night, indicating that light pollution interferes with valuable ecosystem services provided by nocturnal seed dispersers. In particular, experiments with captive *C. sowelli* highlighted that bats performed more explorative flights and harvested fruits more often in a dark than in an illuminated environment. Given the low light intensities used in the experiment, we infer that *C. sowelli* was repelled by intensities even lower than those measured underneath street lights. We therefore suggest that the rapid spread of light pollution might severely affect the spatial foraging behaviour of frugivorous bats. Nocturnal seed dispersers may visit fruiting plants or entire feeding areas less often when these are illuminated by artificial light. Particularly frugivorous bats such as *C. sowelli* depend on many fruiting plants because each plant individual produces only a few ripe infructescences per night. Consequently, bats of the genus *Carollia* search ripe infructescences at numerous plants each night and switch frequently between distant feeding areas when foraging (Fleming 1988).

Our findings with captive bats were consistent with those obtained from free-ranging bats. Wild bats harvested fewer *Piper* infructescences from illuminated *Piper* plants and, when foraging did occur, they removed infructescences from illuminated plants about 2 h later than from plants in complete darkness. This delay in foraging activity may drastically reduce the likelihood of seed dispersal for a plant, particularly when additional adverse conditions reduce the activity of bats later at night, for example during tropical rainfalls (Voigt *et al.* 2011). Further, if a *Piper* infructescence is not harvested during the first night after ripening, it may not be removed and may fall to the ground (Thies & Kalko 2004). Irrespective of whether an illuminated infructescence is harvested later at night or whether it is completely neglected and not removed at all, in both circumstances, the avoidance behaviour of frugivorous bats towards artificial light at night reduces the probability of successful seed dispersal. This has major implications for ecosystem functioning when tropical habitats are increasingly exposed to artificial light. Bat-dispersed successional plants in particular, such as Piperaceae and Solanaceae, might suffer from a reduced visitation rate in an illuminated environment. Due to their preference for disturbed areas, pioneer plants are more likely exposed to artificial light, for example, when street lights are established along roads or when lights at buildings illuminate the surroundings at night.

Anthropogenic disturbance *per se* may not necessarily reduce bat abundance and the associated ecosystem services, because some bat species are relatively resistant to fragmentation. Many frugivorous bat species fly up to 2·5 km across open areas in the Neotropics (Bernard & Fenton 2003) and some species which are specialized on pioneer plants might even be more abundant in disturbed habitats (Willig *et al.* 2007). These bats are important for the rapid succession in clearings because they produce a copious seed rain even in deforested areas such as abandoned pastures (Medellin & Gaona 1999). In the Neotropics, the majority of cleared lowland forest becomes pasture but more than 50% of the clearings in the Amazon are abandoned within 10 years because of the poor fertility of tropical soils (Hecht 1993). Here, bat-mediated seed intake could promote reforestation and reduce the many negative outcomes associated with abandonment such as pronounced land erosion which may cause landslides, runoff, water loss, leaching and siltation of streams and rivers. However, the ability of a species to resist anthropogenic disturbance depends on the nature and the level of disturbance. Although frugivorous bats might easily traverse open areas between forest fragments in naturally dark nights, our results suggest that they are less likely to use habitats which are 'polluted' by artificial light at night. It appears that artificial light constitutes a severe anthropogenic disruptive factor which affects even species that are tolerant to fragmentation or other anthropogenic changes to ecosystems. Accordingly, succession with pioneer plants may slow down in areas with artificial light and habitat loss may be aggravated for light-sensitive species. This may result in cascading effects that could prove expensive for landowners and communities.

Artificial light from villages and street lamps may serve as a 'light barrier' that inhibits light-sensitive bats from conducting long-distance seed dispersal and pollination services between remaining forest fragments and therefore increases the degree of isolation. The light-barrier argument goes beyond what can be directly inferred from our experiment, but it seems plausible given the fact that street lights are usually brighter than the 4·5 lux used in our experiment. Also, bats of the genus Carollia usually fly at low heights above-ground (Rex *et al.* 2011) and may therefore be unwilling to cross illuminated streets above the glare of lamps. Some support for a light-barrier effect comes from a study which showed that the few frugivorous bat species which do occur in urban areas can rarely be captured along roads (Oprea *et al.* 2009). Further, even some insectivorous bats that could potentially benefit from feeding on insects attracted to street lights avoid roads more than other urban land cover classes when commuting (Davies, Hale & Sadler 2012) or do not commute in the catchment area of street lights at all (Stone, Jones & Harris 2009, 2012). If commuting of frugivorous bats is affected in a similar way by light barriers, then artificial light at night might not only lead to genetic isolation of illuminated plants and to a loss of suitable habitats for light-sensitive species but could also hinder seed exchange and genetic connectivity between whole forest fragments (Jordano *et al.* 2011). Then, maintenance of biodiversity and finally ecosystem functioning could be at risk in areas composed of forest remnants embedded in a matrix without sufficiently dark corridors. Possibly, such a scenario may be realized in many tropical countries, as both deforestation and light pollution proceed at high rates across the tropical climate domain (Hölker *et al.* 2010; FAO & JRC 2012).

On a global scale, bats are known to disperse seeds not only of *Piper* but also seeds of hundreds of other tropical tree and shrub species that support biodiversity (Thomas 1991). In addition, many agriculturally produced fruits such as mango and shea as well as many economically relevant timber species are pollinated or dispersed by bats (Ghanem & Voigt 2012). The production of shea trees (a bat-dispersed species) was estimated to exceed 2·5 million metric tons each year (Lovett 2005), highlighting the relevance of bats as seed dispersers for species used by humans. Artificial light at night may severely affect these economies when pollinating and seed-dispersing services of bats are reduced.

Problems associated with artificial light may become even more aggravated on a larger geographical scale, considering that light pollution is increasing rapidly at an annual rate of about 6% world-wide (Hölker *et al.* 2010). Since the degree of light pollution parallels population growth and economic development (e.g. Elvidge *et al.* 2001), it can further be expected that artificial light at night increases at exceptionally high rates in many tropical countries. For example, the outdoor lighting market in Latin America is estimated to nearly double between 2010 and 2020 (Baumgartner *et al.* 2011). Due to the exponential growth rate of human populations in many tropical countries (UNPF state of world population 2011), people will encroach further into formerly pristine habitats than ever before. Since this encroachment is probably accompanied by an intensified use of artificial light, it might have deleterious consequences for nocturnal seed dispersal and habitat connectivity.

CONCLUSIONS & RECOMMENDATIONS

We conclude that the detrimental effects of light pollution are likely to increase and may have a great impact on biodiversity, particularly in the tropics where artificial light follows human encroachment in natural habitats at unprecedented rates.

Policy-makers should pay attention to the ecological impacts of artificial light, and policy should ensure artificial light is not excessively used. To mitigate the negative effects, artificial light should be restricted to (i) where it is needed, (ii) when it is needed and to (iii) an illumination level that achieves its purpose but does not exceed it. Particularly in the tropics, where nocturnal seed dispersers are crucial for ecosystem functioning, maintaining unlit

habitats large enough to guarantee viable populations of light-sensitive species should be of high priority, since even very low light intensities were sufficient to reduce the foraging activity of fruit-eating bats. To achieve this, it is essential to raise awareness of the ecological impacts of artificial light by informing people and policy about the deleterious effects light pollution can have on a wide range of taxa (reviewed in Rich & Longcore 2006).

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