THE INFLUENCE OF URBANIZATION AND SURROUNDING LANDSCAPE ON WILDLIFE IN NATURAL AREAS

By

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ABSTRACT OF THE DISSERTATION THE INFLUENCE OF URBANIZATION AND SURROUNDING LANDSCAPE ON WILDLIFE IN NATURAL AREAS

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Urbanization is a leading driver in habitat loss and land-use change. As large swaths of natural areas are developed, conservationists and city planners set aside land for the protection of wildlife and the health of citizens. However, areas set aside for conservation are not immune to influence of surrounding land-use changes and other impacts associated with urbanization. This dissertation investigates how changes in the surrounding landscape influence wildlife communities in natural areas. First, I explore how increased levels of development and the increase in nonnative species associated with this development influence songbird communities within a protected forest over time. Next, I investigate different measures of bird biodiversity within protected forests and highlight how these metrics vary with the size of the protected forest as well as the landscape surrounding the forest. Lastly, I highlight how the introduction of artificial light at night, a common disruption associated with urbanization, shifts arthropod communities in a natural forest. The work from this dissertation emphasizes the importance of understanding the dynamics occurring outside of protected and natural spaces and incorporating these dynamics into future conservation plans.

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Introduction

As of 2019, nearly 8 billion people live on the plant and over 50% of them live within urban centers (U.N. D.E.S.A. 2017). Population growth in these urban areas is significantly higher than in other parts of the world and by 2050 the human population is expected to reach 9 billion with 70% of individuals living in urbanized landscapes (Lutz et al. 2001; DeFries et al. 2010; U.N.P.D. 2018). Unfortunately, this rapid urbanization comes at a high cost to biodiversity and human health. Expanding cities threaten to convert natural areas resulting in a reduction of habitat for biodiversity and the loss of access to nature for urban residents (Cincotta et al. 2000, Brooks et al. 2002, Jennings et al. 2012). To combat these problems, conservationists and city planners turn to the preservation of open spaces within cities.

Open spaces service two major purposes within urban environments. One of the primary purposes of open spaces is the conservation of wildlife through the preservation of habitat. Within urban areas, open spaces typically have increased species diversity and richness when compared to non-protected areas but this pattern varies greatly due to the heterogenic nature of developed areas (Naughton-Treves et al. 2005, Goddard et al. 2010, Kong et al. 2010). While the patterns associated with urban biodiversity are still under investigation, recent work highlighting biodiversity within cities calls for an increased need for urban conservation efforts (Donnelly and Marzluff 2004, Dudley 2008, Aronson et al. 2014). Current research in the area suggests the of the largest factors influencing protected areas in urban areas are a limitation of size and proximity to development (Goddard et al. 2010, Kong et al. 2010, Smith et al. 2010). It unrealistic to protect large swaths of land in most developed spaces because they do not exist, so instead we must focus on how smaller reserves will function and how to best manage them (Donnelly and Marzluff 2004). We also must understand how proximity to development impacts protected areas (Radeloff et al. 2010). By investigating how both size and landscape influence protected areas, we can more effectively protect species in urban settings. This protection in turn helps serve the second goal of urban open spaces.

In addition to protecting wildlife, urban open spaces also serve a critical role in connecting urban residents with nature (Miller 2005; Corraliza et al. 2012). For many urban residents, open spaces provide their only access to nature which in turn influences their views on conservation as well as their physical and mental health (Jennings et al. 2012; Lovell et al. 2014; Shanahan et al. 2015). Just as the size and surrounding matrix of an open space influence the wildlife within it, it also impacts visitors' experiences and perceptions of open spaces (Vinning et al. 2008; Shwartz et al. 2014). These perceptions are further influenced by the artificial features within open spaces. Many features that increase visitors' perceptions of open spaces negatively impact wildlife (Longcore and Rich 2006). This direct conflict coupled with the dual purpose of open spaces calls into question how well urban green spaces accomplish their goals.

To understand how urban open spaces function, this dissertation investigates how communities within these open spaces change over time, throughout landscapes, and in response to disturbance. Urban environments are highly heterogenic and although the open space may stay static, changes in the surrounding landscape can have strong impacts on communities within the open space. These changes are seen when landscapes develop over time because of increasing population and are also observed when comparing open spaces in different matrixes. Finally, disturbances that penetrate open spaces, such as light pollution, strongly influence communities within these areas.

This dissertation is divided into three chapters which are introduced below. All three of the chapters are co-authored by my advisor Julie Lockwood. All chapters have additional co-authors which are specified in their summaries below.

Evaluating the long-term effectiveness of terrestrial protected areas: a 40-year look at forest bird diversity

Through the actions of the CBD, government agencies, and other land conservation groups, approximately 14% of the global terrestrial area now has protected status (IUCN 2016). However, it is unclear how many of these terrestrial areas function in protecting biodiversity (Bruner et al. 2004). A principal concern is whether the existing (and future) portfolio of protected areas will perform well over the long-term in their ability to stave off species extinction (Gaston et al. 2008; Rayner et al. 2014).

Our understanding of how well protected areas maintain species diversity is hindered by the difficulty involved in obtaining informative datasets (Tingley and Beissinger 2009; Metcalfe et al. 2013). Biodiversity surveys are expensive and difficult to sustain over long time periods (Tingley and Beissinger 2009; Iknayan et al. 2014). Of the few studies that have tracked the fate of biodiversity in protected areas through time, most span a decade or less (DeFries et al. 2005; Rayner et al. 2014; Geldmann et al. 2015). Arguably, it is the longer time scales (decades) that are most relevant for evaluating protected area effectiveness as it reflects the ability of the site to sustain biodiversity in the face of the large-scale and long-term threats that are most detrimental to species (e.g., land use conversion, invasive species, over-harvesting, climate change) (Ando et al. 1998; Mooney and Cleland 2001; Hannah et al. 2007; Sparks 2007; Maiorano et al. 2008). Additional gaps in our understanding of protected area performance stem from the

lack of quantitative assessments of protected temperate forests.

One solution to filling these knowledge gaps is to initiate long-term biodiversity monitoring schemes for recently established protected areas to evaluate effectiveness in the future. Another more immediate solution is to extract archival data on species' use of sites set aside for protection decades ago. When this archival data is combined with contemporary information, researchers can directly evaluate species persistence and correlate loss (or gain) of species over time to specific mechanisms such as habitat loss, poaching, or disease.

In this chapter we explore the performance of a forested protected area in terms of its ability to sustain avian diversity over a 40-year time span. Hutcheson Memorial Forest (HMF), a rare example of an uncut old growth deciduous forest in the US, was originally set aside explicitly for its ecological value in 1955. Because of its affiliation with Rutgers University, it was the subject of an intensive 8-year effort involving repeat within-season monitoring of breeding passerine birds shortly after its preservation. We closely matched these monitoring efforts over a comparable period starting in 2009. These two datasets provide a unique re-visitation study of the effectiveness of forest protection for 40 years while explicitly accounting for detection bias. We also use these data, combined with regional breeding bird trends, to assess how the site is performing relative to regional population trends. Although a single site, it is very typical of protected areas established in the last decade worldwide in that 68% of the 35,694 terrestrial protected areas added to the World Protected Area Network from 2007-2017 are of equal or smaller size to HMF (UNEP-WCMC 2017). HMF also shares similarities with many modern protected areas as it has no active management programs and was left largely untouched by those who placed it into protection (Geldmann et al. 2015).

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Protected forests provide varied biodiversity experiences within an urban landscape

By 2050 nearly 70% of the world's population will live in urban areas (United Nations Department of Economic and Social Affairs, 2018), resulting in an at least 15.5 million km² of land being converted for urban land uses (Seto, Güneralp, & Hutyra, 2012). As urbanization increases, many people lose access to nature, resulting in a decrease in their physical and mental health (Chiesura, 2004; Gilbert & Phillips, 2003; Nielsen & Hansen, 2007). One solution to this dilemma is for urban planners to protect natural habitat as open spaces allowing urban residents easy and direct interactions with the living world (Jennings, Johnson Gaither, & Gragg, 2012). While evidence shows a link between access to nature and increased wellness, this link is complex and poorly understood (Pett et al. 2016).

Currently, most research effort attempting to explain the relationship between nature and human wellbeing focuses on how people respond to species richness. This research uses simple tallies of species present (i.e., species richness), or in terms of the presence of broad functional groups (e.g., cavity nesting birds or colorful flowers; Cox & Gaston, 2015; Dallimer et al., 2012). However, further investigation into this link shows that while richness is correlated with increased human health, people are unable to identify indictors of species rich areas (Pett, Shwartz, Irvine, Dallimer, & Davies, 2016; Shwartz, Turbé, Simon, & Julliard, 2014). This so-called 'people-biodiversity paradox' reflects the varied dimensions through which people perceive and respond to natural environments, and how these responses are themselves determined by individual cultural, economic, and experiential backgrounds (Shwartz et al., 2014). There has been surprisingly little exploration, however, of the multi-dimensionality of the biodiversity side of this paradox, leaving a significant gap in our ability to 'unpick' the paradoxical knot that ties human health and species richness (Pett et al., 2016).

In this chapter, we explored several aspects of avian biodiversity within urban forested protected areas within the New Jersey Highlands (USA) to investigate the different ways biodiversity presents itself to visitors. Recent research suggests that people respond to nature in ways that link to both species' rarity and uniqueness (Dunn et al. 2006; Louv 2008; Johnson et al. 2010, Fairchild et al. 2018). Following this evidence of how people value and respond to biodiversity, we measured for each forested protected area the (1) total bird species (richness), (2) number of species that are dependent on forested habitat (3) number of species that are regionally rare or of conservation concern, and (4) uniqueness of the bird community within the protected area relative to the community in surrounding unprotected habitat. We measure these metrics across a range of forest sizes and surrounding habitat types to understand how size and matrix influences biodiversity. This information provides insight as to how different forests present biodiversity and lays the groundwork for future investigation of how people value nature.

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Things that go bump in the light: introduction of artificial light at night increases abundance of predators, detritivores, and parasites in arthropod communities

Light pollution and the increase of artificial light at night (ALAN) is a growing threat to global biodiversity. With increases in urbanization and the introduction of new technologies such as LEDs, there are few places left on the planet unimpacted by ALAN (Longcore and Rich 2004, Pawson and Bader 2014). Each year an additional 6% of total land is influenced by nighttime light pollution but the extent of impacts of ALAN are poorly understood (Smith 2008, Hölker et al. 2010, Bennie et al. 2015). Current studies fail to isolate artificial light as mechanistic driver of change since the majority of artificial light research has used urban-rural gradients to compare community composition and species' abundance in areas of high ALAN to areas without ALAN (Rich and Longcore 2006). Other studies have compared individual behaviors seen around artificial lights to behaviors seen in non-light disturbed environments (Polak et al. 2011, Davies et al. 2012, Becker et al. 2013, Gaston et al. 2013), but see for a manipulative experiment (Meyer and Sullivan 2013). In this chapter we specifically investigate light pollution as a source of biodiversity changes. Using an array of pitfall traps and artificial lights, we experimentally investigate how naïve forest arthropod communities (i.e. a community that has not previous experienced light pollution) respond to the introduction of ALAN. Through experimental manipulation, we established ALAN as a mechanistic driver in community change by monitoring compositional change before and after the introduction of artificial light. We continued to sample after the removal of ALAN to investigate if these communities returned to their pre-disturbed state, or if artificial light impacts communities even when it is turned off or has been permanently removed (see Davies et al. 2012). Our results provide insight into how arthropod communities will respond as light pollution spreads to non-light-polluted environments. Additionally, we gain insight into the speed the speed at which communities respond to changes in levels of ALAN.

This chapter was formatted for *Ecology* and will be submitted there:

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References

- Aronson, M. F. J., F. A. L. Sorte, C. H. Nilon, M. Katti, M. A. Goddard, C. A. Lepczyk, P. S. Warren, N. S. G. Williams, S. Cilliers, B. Clarkson, C. Dobbs, R. Dolan, M. Hedblom, S. Klotz, J. L. Kooijmans, I. Kühn, I. MacGregor-Fors, M. McDonnell, U. Mörtberg, P. Pyšek, S. Siebert, J. Sushinsky, P. Werner, and M. Winter. 2014. A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. Proc. R. Soc. B 281:20133330.
- Becker, A., A. K. Whitfield, P. D. Cowley, J. Järnegren, and T. F. Næsje. 2013. Potential effects of artificial light associated with anthropogenic infrastructure on the abundance and foraging behaviour of estuaryassociated fishes. Journal of Applied Ecology 50:43–50.
- Bennie, J., J. P. Duffy, T. W. Davies, M. E. Correa-Cano, and K. J. Gaston. 2015. Global Trends in Exposure to Light Pollution in Natural Terrestrial Ecosystems. Remote Sensing 7:2715–2730.
- Brooks, T. M., R. A. Mittermeier, C. G. Mittermeier, G. A. B. D. Fonseca, A. B. Rylands, W. R. Konstant, P. Flick, J. Pilgrim, S. Oldfield, G. Magin, and C. Hilton-Taylor. 2002. Habitat Loss and Extinction in the Hotspots of Biodiversity. Conservation Biology 16:909–923.
- Cincotta, R. P., J. Wisnewski, and R. Engelman. 2000. Human population in the biodiversity hotspots. Nature 404:990–992.
- Davies, T. W., J. Bennie, and K. J. Gaston. 2012. Street lighting changes the composition of invertebrate communities. Biology Letters:rsbl20120216.
- Donnelly, R., and J. M. Marzluff. 2004. Importance of Reserve Size and Landscape Context to Urban Bird Conservation. Conservation Biology 18:733–745.
- Dudley, N. 2008. Guidelines for Applying Protected Area Management Categories. IUCN.
- Goddard, M. A., A. J. Dougill, and T. G. Benton. 2010. Scaling up from gardens: biodiversity conservation in urban environments. Trends in Ecology & Evolution 25:90–98.
- Hölker, F., C. Wolter, E. K. Perkin, and K. Tockner. 2010. Light pollution as a biodiversity threat. Trends in Ecology & Evolution 25:681–682.
- Jennings, V., C. Johnson Gaither, and R. S. Gragg. 2012. Promoting Environmental Justice Through Urban Green Space Access: A Synopsis. Environmental Justice 5:1–7.
- Kong, F., H. Yin, N. Nakagoshi, and Y. Zong. 2010. Urban green space network development for biodiversity conservation: Identification based on graph theory and gravity modeling. Landscape and Urban Planning 95:16–27.
- Longcore, T., and C. Rich. 2004. Ecological Light Pollution. Frontiers in Ecology and the Environment 2:191–198.
- Lutz, W., W. Sanderson, and S. Scherbov. 2001. The end of world population growth. Nature 412:543–545.
- Meyer, L. A., and S. M. P. Sullivan. 2013. Bright lights, big city: influences of ecological light pollution on reciprocal stream–riparian invertebrate fluxes. Ecological Applications 23:1322–1330.

- Naughton-Treves, L., M. B. Holland, and K. Brandon. 2005. The Role of Protected Areas in Conserving Biodiversity and Sustaining Local Livelihoods. Annual Review of Environment and Resources 30:219–252.
- Pawson, S. M., and M. K.-F. Bader. 2014. LED lighting increases the ecological impact of light pollution irrespective of color temperature. Ecological Applications 24:1561–1568.
- Polak, T., C. Korine, S. Yair, and M. W. Holderied. 2011. Differential effects of artificial lighting on flight and foraging behaviour of two sympatric bat species in a desert. Journal of Zoology 285:21–27.
- Radeloff, V. C., S. I. Stewart, T. J. Hawbaker, U. Gimmi, A. M. Pidgeon, C. H. Flather, R. B. Hammer, and D. P. Helmers. 2010. Housing growth in and near United States protected areas limits their conservation value. Proceedings of the National Academy of Sciences 107:940–945.
- Smith, M. 2008. Time to turn off the lights. Nature 457:27.
- Smith, R. J., E. D. Minin, S. Linke, D. B. Segan, and H. P. Possingham. 2010. An approach for ensuring minimum protected area size in systematic conservation planning. Biological Conservation 143:2525–2531.
- The World Population Prospects: 2015 Revision. 2015. . Report.
- World Population Prospects: The 2017 Revision. 2017. . United Nations Department of Economic and Social Affairs.

Evaluating the long-term effectiveness of terrestrial protected areas: a 40-

year look at forest bird diversity

Abstract

Designation of protected areas has become one of the primary approaches to reducing biodiversity loss, with the number of new set-asides growing in the last decades largely from the addition of small protected areas to the global portfolio. Information on the effectiveness of protected areas to stave off species extinction is surprisingly scarce, with almost nothing known about the long-term fate of biodiversity in smaller protected temperate forests. Here we use an uncommonly complete biodiversity inventory of a small protected deciduous forest to evaluate its performance over a 40-year time span. We tracked bird compositional changes using a within-season repeat sampling protocol allowing us unusual accuracy in documenting species gains and losses through time. We found that nearly half the species found in the forest at the time of initial protection are now extirpated, and that yearly forest species composition is highly dynamic. Ground nesting and migratory species were more likely to be extirpated than were canopy breeders, cavity nesters, and year-round residents. Regional population declines explained differences in extirpation probability across species indicating that the study population, to some extent, mirrored larger regional dynamics. However, a substantial number of species declined in abundance within the forest while experiencing no regional declines, or even regional increases, in abundance. Our results reinforce that even with protected status, small forest fragments may not provide the conservation benefits that protection is meant to provide. Keywords: conservation, forest bird, long-term monitoring, protected area, forest

management, urban forest

1. Introduction

Conservation targets set by the Convention on Biological Diversity (CBD) are arguably the most globally significant actions taken to protect biodiversity (Venter et al. 2017). A primary goal of the CBD is to establish protected areas as a means to prevent species extinction (Watson et al. 2014). Through the actions of the CBD, government agencies, and other land conservation groups, approximately 14% of the global terrestrial area now has protected status (IUCN 2016). However, there are several informational gaps that prevent us from declaring this an unequivocal success (Bruner et al. 2004). A principal concern is whether the existing (and future) portfolio of protected areas will perform well over the long-term in their ability to stave off species extinction (Gaston et al. 2008; Rayner et al. 2014). Most efforts to evaluate conservation success use surrogates for biodiversity (e.g., management schemes or habitat integrity) that may not be reliable indicators of the true fate of species relying upon the site (Chape et al. 2005; Coetzee et al. 2014; Rayner et al. 2014). More direct assessments document how species composition within a protected area changes through time, as well as compare trends in species' populations within and outside the protected area (Rayner et al. 2014). In a wideranging review of protected area effectiveness, Gaston et al. (2008) found that < 5%of published research had followed either of these approaches, revealing a substantial knowledge gap. To help fill this void, we evaluated the biodiversity effectiveness of a small isolated old-growth deciduous forest under protection since 1955. We used bird banding records spanning the period this site has been protected to create a unique and robust long-term assessment of which species have benefited from protection, and which have not.

Our understanding of how well protected areas maintain species diversity is hindered by the difficulty involved in obtaining informative datasets (Tingley and Beissinger 2009; Metcalfe et al. 2013). Biodiversity surveys are expensive and difficult to sustain over long time periods (Tingley and Beissinger 2009; Iknayan et al. 2014). Of the few studies that have tracked the fate of biodiversity in protected areas through time, most span a decade or less (DeFries et al. 2005; Rayner et al. 2014; Geldmann et al. 2015). Arguably, it is the longer time scales (decades) that are most relevant for evaluating protected area effectiveness as it reflects the ability of the site to sustain biodiversity in the face of the large-scale and long-term threats that are most detrimental to species (e.g., land use conversion, invasive species, over-harvesting, climate change) (Ando et al. 1998; Mooney and Cleland 2001; Hannah et al. 2007; Sparks 2007; Maiorano et al. 2008).

Additional gaps in our understanding of protected area performance stem from the lack of quantitative assessments of protected temperate forests. Although the number of protected areas continues to increase globally, the majority of these areas go unevaluated and most published research has centered on the fate of biodiversity within tropical ecosystems (Western et al. 2009; Sigel et al. 2010; Laurance et al. 2012; UNEP-WCMC 2017). This body of research indicates that protected areas are becoming more isolated over time, and when these areas are also small in size, they fail to conserve species over the long-term (DeFries et al. 2005; Gurd et al. 2008). There is, however, very little evidence to show if this pattern is also true for temperate forests (DeFries et al. 2005; McDonald et al. 2008).

One solution to filling these knowledge gaps is to initiate long-term biodiversity monitoring schemes for recently established protected areas to evaluate effectiveness in the future. Another more immediate solution is to extract archival data on species' use of sites set aside for protection decades ago. When this archival data is combined with contemporary information, researchers can directly evaluate species persistence and correlate loss (or gain) of species over time to specific mechanisms such as habitat loss, poaching, or disease. Such 're-visitation' approaches have been successfully used by several researchers to detect long-term biodiversity trends outside of protected areas (Edwards et al. 2007; Hobbs et al. 2007; Tingley and Beissinger 2009). However, this approach has rarely been used to judge the effectiveness of protected areas (c.f., Sigel et al. 2006, 2010 for examples in the tropics). The lack of resampling studies may stem from an absence of archival datasets, or a lack of sites under protection for enough time to allow such an evaluation.

Even when archival and contemporary data on species' use of a site exists, there are known pitfalls associated with using this information that must be explicitly addressed before making sound inferences (Kéry et al. 2006; Tingley and Beissinger 2009; Iknayan et al. 2014). We suggest that these pitfalls, including lack of detection probability and incomplete records, take on added relevance when revisitation data are used to evaluate the effectiveness of protected areas. In revisitation studies, researchers often cannot directly estimate species' detection probability, and thus cannot adequately shed light on the presence or absence of rare species (Kissling and Garton 2006). In the context of protected areas, a site will be deemed highly effective if it maintains a substantial proportion of the species it held at the time of original protection. The loss of any native species, especially those rare and/or threatened with extinction at the time of protection, will signal ineffectiveness. Thus, without an understanding of detection rates, and how they vary between species and through time, we risk failing to detect species loss when it occurred or declaring species loss when it did not occur. These two sources of error, if unaccounted for, present the real possibility of producing biased assessments of protected area effectiveness.

Here we explore the performance of a forested protected area in terms of its ability to sustain avian diversity over a 40-year time span. Hutcheson Memorial Forest (HMF), a rare example of an uncut old growth deciduous forest in the US, was originally set aside explicitly for its ecological value in 1955. Because of its affiliation with Rutgers University, it was the subject of an intensive 8-year effort involving repeat within-season monitoring of breeding passerine birds shortly after its preservation. We closely matched these monitoring efforts over a comparable period starting in 2009. These two datasets provide a unique re-visitation study of the effectiveness of forest protection for 40 years while explicitly accounting for detection bias. We also use these data, combined with regional breeding bird trends, to assess how the site is performing relative to regional population trends. Although a single site, it is very typical of protected areas established in the last decade worldwide in that 68% of the 35,694 terrestrial protected areas added to the World Protected Area Network from 2007-2017 are of equal or smaller size to HMF (UNEP-WCMC 2017). HMF also shares similarities with many modern protected areas as it has no active management programs and was left largely untouched by those who placed it into protection (Geldmann et al. 2015).

2. Methods and Materials

2.1 Study Site

Hutcheson Memorial Forest (HMF) is a 200 ha patchwork of abandoned agricultural fields and uncut old growth deciduous forest located in Somerset County, New

Jersey, USA. We focused on the 26 ha of old growth forest located in the middle of HMF as this was the location of prior banding efforts. Oak and hickory trees dominate the old growth section of the forest with trees averaging 200 years old and some individuals still standing after 350 years, making it an exceptionally rare habitat (Buell 1957; Davis 2008). In the past 60 years, HMF has experienced invasion of non-native plants in the understory as well as a decrease in overall shrub cover (Aronson 2007, Aronson et al. unpublished data). Until 2016, there was no active management of the old growth forest. No living trees were harvested from the forest. White-tailed deer (*Odocoileus virginianus*) were estimated at 58-77 deer per square kilometer in 2011 (Aronson and Handel 2011). HMF is surrounded by agricultural and residential landcover and there are no forests larger than 100 ha within 5 km.

Using a combination of aerial photos as well as GIS images taken decennially from 1956 until 2012, we assessed habitat change at the direct border of HMF and within a 3 km buffer around the forest edge. At each of the two time periods, the landscape within the 3 km buffer (including right at the border) was classified into six land use – land cover (LULC) groups using existing United States Geological Survey (USGS) designations (Table 1). We tracked the percent change in these six classes between 1960 to 2015 to document changes in LULC.

2.2 Temporal Dynamics of Forest Species

Dr. Jeff Swinebroad, a former Rutgers professor, began an extensive bird banding effort at HMF in 1960 and continued this effort annually until 1967. He and his colleagues established a 100 m² grid within the old growth forest and placed 10 to 14 mist nets within a subset of these grid cells on every capture occasion. They opened the nets and captured birds within HMF on at least six separate occasions within every breeding season (May-July).

With the assistance of a participant of the earlier banding efforts (B. Murray), we re-established 12 net locations in the old growth forest that were regularly used by Swinebroad in the 1960s. We began our banding efforts in 2009 and continued annually until 2015. We followed the earlier protocol as closely as possible in order to make direct comparisons between current and historical data (Leck et al. 1988). This included matching capture effort with historical effort by using the same net dimensions and mesh size, number of days in-between net deployment (every 5 to 10 days), and the time of day and length of time when nets were active (sunrise plus 5 h). When nets were not in use they were completely removed, and banding effort was restricted to days without rain and without wind exceeding steady levels of 10 mph (Ralph et al. 1993). Nets were 2.6 m high by 12 m long, and had 30 mm mesh size, allowing for the capture of species as small as warblers. Nets were left open between 6 am and 11 am, and participants checked nets for captured birds every 30-45 minutes.

In all banding efforts, no matter the time period, all captured birds were given a USGS unique number leg band before release. Through these efforts we have detailed banding data spanning a total of fifteen years; eight years from 1960-1967 (historical data) and seven years from 2009-2015 (current data). Any species that do not breed within forested habitats were removed (e.g., grassland species incidentally captured at the forest edge). Mist nets are known to capture only forest birds that visit the understory or low canopy (Blake and Loiselle 2001; Wang and Finch 2002) and our results pertain only to this group. Our data reflects 306 banding days and 4,328 capture events. These 4,328 captures represent 68 species and 2,396 unique individuals. We recaptured 770 individuals and of these 399 were captured two or more times. No individuals banded in the historical time period (1960-1967) were recaptured in the current time period, which is unsurprising given the majority of species captured have longevities of <10 years. Over 80% of all species captured had fewer than 10% of their individuals recaptured within a single breeding season. This low level of within-season recaptures prevented us from using standard markrecapture methods to evaluate changes in population size either within, or across, time periods. However, we used the number of unique individuals captured of a given species as a proxy for possible minimum population size.

We combined within-season capture records from individuals of the same species to create annual presence-absence histories of species' use of the forest. If a single individual of a species was captured on a given day we counted that species as 'present' in that sampling event (day) and 'absent' otherwise. Since we are primarily interested in whether species are present within the forest, we compiled banding records for all individuals of the same species across all days of banding in a single breeding season (six to eight banding events per season) allowing us to calculate detection probability per year and per species. Following MacKenzie et al. (2002), we defined detection probability (p) as the proportion of sampling events within a single time frame (here a breeding season) for which a species was present. In the historical period (1960-1967) we had 47 total sampling events with an average of seven sampling events per year. In the current period (2009-2015) we had 41 different sampling events with an average of six sampling events per year. Thus, for both time periods, we could observe species with detection probabilities (p) at least as low as 0.17. This rich dataset allowed us to compare how species' presence changes over time and to examine shifts in detection probability across time periods. Also, since we had very similar detection effort levels across time periods, we could safely assume that any observed change in species' detection probabilities across time periods represented an underlying change in species' population size. For all further analyses, we removed species from consideration if their breeding range or habitat did not overlap with HMF according to maps produced by Cornell Lab of Ornithology (Rodewald 2015) as these tended to represent one-time incidental captures.

We documented changes in species' use of the forest through time by calculating the average number of species found in the forest at each time period. Species richness was calculated by taking the average species richness across all years within a time period. We also calculated temporal turnover in species composition between all possible pairs of consecutive years, where a value of 1 indicates complete species turnover and a value of 0 indicates no difference in community composition between the two years. Finally, we compared the species composition of HMF between time periods using non-metric multidimensional scaling in the R 3.3.3 package Vegan (Oksanen et al. 2017). We used hierarchical clustering to determine the similarity of bird communities across time periods, and confirmed cluster membership using a multivariate bootstrapping routine (Podani 1994).

Next we created a generalized linear mixed model to investigate if life history traits, minimum historical population size, or USGS Breeding Bird Survey (BBS) regional population trends explained change in species' occupancy rates between time frames (Sauer et al. 2017). We considered occupancy rate to be the percentage of years in which a species occupied (i.e., was present within) each time period. For example, a species that occupied HMF in all current years (2009-2015) would have a calculated occupancy rate of 7/7 or 100%, whereas a species that occupied the forest for only one year would have a rate of 1/7 (14%). We calculated per species change in occupancy rates by subtracting current species' occupancy rates from historic species' occupancy rates.

The full model predicted change in occupancy rate based on migratory status (binary), nesting location (categorical), foraging behavior (categorical), habitat preference (categorical), diet (categorical), initial minimum population size (continuous), and regional growth rate from BBS (continuous) (Table S1). We recorded life history traits from the Cornell Lab of Ornithology (https://birdsna.org/, 2016) for each species and considered them fixed variables for our model. We included as random variables the minimum number of individuals captured in the historical time period as an index of each species' population size at the time of protection designation, and the 40-year regional growth trends from the BBS (see below for calculations). We evaluated the full model and all its permutations for a total of 128 models. Model quality was compared using AICc, and we selected models with $\Delta AICc < 2$ as the best of the set. Following Burnham and Anderson (2002), we employed model averaging of the top performing models to determine average effect sizes and their relative importance. We used the package MuMin in R version 3.3.3 for this analysis (Barton 2018). Finally, McFadden's pseudo R² value was calculated and weighted for each model to find an average goodness of fit of the averaged model (Veall and Zimmermann 1996; Cameron and Windmeijer 2012).

2.3 Comparing Species Fate Inside and Outside the Protected Forest

Protected areas are established, in part, as safe havens for species experiencing regional declines (Rodrigues et al. 2004). Thus, a critical evaluation of protected area effectiveness should compare species' populations inside versus outside protected areas. We did not have detailed banding records outside of HMF that match our temporal efforts within HMF. However, we compared the population sizes of the species within HMF to regional trends in abundance over the time frame of our banding records (1960s to 2010s). To do so we estimated regional population abundance trends from 1966 and 2012 using BBS data for all of New Jersey (Sauer et al. 2017). The Breeding Bird Survey uses repeat sampling along transects to estimate population abundance trends. The BBS contained enough abundance information to calculate robust regional trends for 41 of the 68 species captured within HMF (Table S2). We used the USGS website trend analysis routine to calculate annual estimates of abundance change and 95% confidence intervals around these annual estimates (Link and Sauer 1998; Sauer 2011). No BBS routes overlapped with HMF.

For the 41 species with sufficient BBS data, we next compared the regional abundance changes to those observed within HMF. Since all species captured within HMF had very low rates of recapture we could not use mark-recapture methods to estimate population size in either time period (having very low recapture rates tends to inflate estimated population sizes, [Roff 1973; Pollock 1982; Fujiwara and Caswell 2002]. Instead we considered the total number of unique individuals of a species captured as a proxy for minimum population size. Starting from a species' minimum abundance calculated using 1960-1967 banding data, we incremented this abundance per annum at a rate equal to the species' regional BBS trend. Given that there is a minimum of 42 years between time periods, we incremented abundance for each of the 41 species across 42 time steps and considered the resulting abundance estimate their predicted minimum abundance within HMF in the current

time period. We repeated this process using the upper and lower 95% confidence intervals (CI) for these annual abundance changes, thus producing a range of possible current minimum abundance estimates for each of the 41 species. For example, if our data for Species A within HMF showed that the lowest number of individuals captured between 1960-1967 was 10, and the BBS regional trend estimate was a 2% increase per year, we estimated a minimum of $10(1.02^{42}) = 23$ individuals in 2009-2015. Assuming that the upper CI from the BBS data gave an annual percentage change of 3% and the lower a percentage change of 1%, we produced a predicted high and low abundance in the current time period of 34 and 15 individuals. Using this method, we compared the expected number of individuals in the current time period to the observed number of individuals captured. If the observed abundance falls outside the range of expected values we can say that species within HMF are faring better or worse than their regional trends would predict. For no species was the projected abundance larger than the number of pairs that could maximally be found in a forest patch the size of HMF using https://birdsna.org/ 2016 estimates of territory size for each species.

3. Results

At the time of acquisition, HMF was surrounded by agricultural fields. Aerial images from 1973 and 2015 show that 44% of the land on the perimeter of the forest changed from agriculture or hayfields to early successional forest (reforestation). Within the 3 km buffer around HMF, we show a 30% loss of agricultural land, the majority of which converted into low density residential housing, with a smaller portion growing into secondary forest (Table 1). Historical average species richness was 23 (sd = 6.71) whereas current species richness is 14 (sd = 2.64). While a total of 16 species are no longer present in the current time period, detection probabilities were low enough in the historical time period for seven of them that we could not unequivocally state that they are now extirpated. However, for the remaining nine species, the failure to capture a single individual in the current time period is well below detection probability estimates derived from the historical record. Researchers recorded only one nonnative species in the forest (European starling, *Sturnus vulgaris*) during the historic period. During this time, a single individual was recaptured multiple times over multiple years. There were no non-natives captured during the current time period, including starlings. Additionally, there were no species found in the current but not historical time period (i.e. no additions).

This loss of species through time led to a shift in community composition (Figure 2). Species that were often present in the historical time period are no longer present (e.g., ovenbird, *Seiurus aurocapilla*, brown thrasher, *Toxostoma rufum*, and red-eyed vireo, *Vireo olivaceus*, Table S2). Additionally, some species that were less common historically are now very common (e.g., common yellowthroat, *Geothlypis trichas*, and hairy woodpecker, *Dryobates villosus*, Table S2). We show that historical and current species composition is quite dynamic with average annual turnover rate of 0.58 (standard deviation 0.13) and 0.47 (standard deviation 0.10) respectively. Our high rates of turnover represent differences in species composition of as many as 15 species from year to year historically and 11 species currently.

The detection probability averaged across species was p=0.24 (sd = 0.07) in the historic time period, which did not differ from the current average across species detection probability of p=0.30 (sd = 0.09). Incorporating this information into occupancy calculations, we found that across-species occupancy rate sharply dropped from the historical to current time period (0.57 historical to 0.36 current). This result held when we calculated occupancy per species where rates dropped by an average of -0.22 between time periods (Table S2). We found that seven models fitted our data on change in occupancy rates well, with three factors explaining most variance in occupancy change (Table 2). After model averaging, the species most likely to have decreased in occupancy rates nested on the ground (effect size = -0.481) or were migratory (effect size = -0.221). Species also tended to increase or decrease in occupancy in concert with their regional population trends (effect size = 4.17×10^{-2}).

Finally, we found that of the 41 species captured in the forest in the historical time period, 22 were found at current minimum abundances lower than their regional trends would have predicted (Table S2). Of these 22 species, 11 were no longer present within Hutcheson Memorial Forest in the current time period. One third (12 of the 41) species found in the historical time period were as abundant as regional trends would have predicted, with five of these 12 species being extirpated from HMF in the current time period. Only seven species were more abundant than we would have expected based on regional trends (current population is above high estimate given BBS trends; Table S2, Figure 3).

4. Discussion

Since 1955, Hutcheson Memorial Forest has experienced strict prohibitions on resource removal, including hunting and logging, and human influence has been limited to an occasional visitor, scientific study, or minor trail upkeep. The land directly adjacent to the protected forest has reforested since the 1960s, and although much of the agricultural land in the surrounding area was developed, there was very little loss of neighboring forest patches. Since habitat loss is often the driving factor in species loss, the preservation of (and potential increase in) habitat should result in the retention of species (Fahrig 1997; Brooks et al. 2002; Coetzee et al. 2014). Our evidence shows this did not happen over the last 40 years. Instead the forest has lost a third of the bird species that were regularly observed breeding there in the 1960s, substantially altering species composition. Because mist netting samples only a fraction of all birds that breed in forests, our results may underestimate changes in diversity within the forest. Nevertheless, our results add to the small but highly relevant set of studies that directly measure the fate of biodiversity within protected areas (Sigel et al. 2010; Raynor et al. 2013; Wesołowski et al. 2015) by including the small protected temperate forests embedded within urbanizing landscapes that are becoming an increasingly dominant component of the global protected area portfolio (UNEP-WCMC 2017).

We show that species within the protected forest that have declined in occupancy (often to extinction) through time tend to be those that are migratory, ground nesters, and are experiencing regional declines. These results suggest that for many bird species the forest is either too small or spatially isolated to provide a refuge from larger-scale factors. For migratory species that breed in HMF, the protected status of the forest apparently cannot adequately counteract the loss of over-wintering or stop-over habitat in the rest of the species' range (Brown et al. 2005; Faaborg et al. 2010). Migrants may also suffer from an increase in brownheaded cowbird nest parasitism or increased nest predation, both of which increase as forest fragment size decreases (Brittingham and Temple 1983; Jokimäki and Huhta 2000). Increasing human populations in the surrounding area further increase risk to migrants as supplemental feeding during the winter allows resident
species to grow in abundance and outcompete migrants during the breeding season (Robb et al. 2008). Growing human residential populations also introduce risk of predation from pets (Loss et al. 2013). Finally, it is difficult for any forest in the eastern U.S. to escape encroachment of exotic species and their sometimes detrimental effects on wildlife habitat (Lovett et al. 2006). Like most protected deciduous forests in the northeastern U.S. (Fisichelli et al. 2014), HMF experienced a dramatic increase in the presence of invasive plants that transform forest understories (Meiners 2007), and a reduction in the presence of key understory trees due to emerging pathogens (e.g., dogwood anthracnose; Daughtrey and Hibben 1994). Eastern U.S. forests have also experienced a sharp increase in the presence of white-tailed deer since the 1960s with attendant loss of forest understory due to over-browsing (Cote et al. 2004; Baiser et al. 2008).

All of these threats were difficult, if not impossible, for the individuals that set aside HMF to foresee. Nevertheless, such factors have driven regional declines in many forest-dependent birds and have had a profound influence on the understory of HMF (Meiners 2007; Baiser et al. 2008). Species such as the ovenbird, blue-winged warbler (*Vermivora cyanoptera*), and black-and-white warbler (*Mniotilta varia*) that nest on the ground or in the understory are all extirpated from Hutcheson Memorial Forest. Changes in the understory are likely key factors as to why the forest, despite its protected status, has not been more successful at protecting the diversity of birds that breed there.

We found that about half of the bird species now breeding within Hutcheson Memorial Forest have declined in abundance at the same rate that they have declined regionally. For the other half we show that the forest seems to be providing resources that are distinctly different from what they are experiencing region-wide (Virkkala et al. 2014). The evidence for conservation effectiveness in this regard, however, is mixed. On the positive side of the conservation ledger, we show that nine species are either not declining in the forest despite a regional decline in their abundance, or are increasing in population despite declining or stable regional trends. In either case, this evidence suggests that the forest is effectively reducing the chances that these species will become locally extinct. On the negative side of the ledger, we show that eight species have either declined at rates far faster than they have experienced regionally, or have declined within HMF despite regionally stable abundance trends. This evidence suggests that the ecological changes within the forest run counter to the biodiversity goals associated with protection status. It is not clear why HMF is performing worse than regional trends would dictate for some species. This trend is clearly worth further investigation, especially if it proves common across the many small protected areas that are being added globally.

Finally, the turnover in the composition of breeding birds within Hutcheson Memorial Forest is consistent between the historical and current time periods despite fewer species being present in the latter period. The low detection probability of some species in the historical time period means our lower estimated turnover during this decade may be a product of not detecting a species in a given year. Since all species in the current time period have detection probabilities above 0.17, our turnover estimate is more accurate. With this caveat, today nearly one third of the species present in a given year may not be present the following year. This 30% turnover rate falls within the range observed for birds living in small habitat fragments and non-isolated islands (between 24-60%) while turnover for vertebrates in undisturbed habitat ranges from 1-10% (Diamond 1969; Schoener 1983). Bird species that breed in small forest patches tend to have small local populations making them susceptible to stochastic extinction events (Whitcomb et al. 1981; Opdam 1991; Andrén 1996). Within landscapes that have only small forest remnants, the regional pool of forest-breeding birds declines and migrants become less likely to encounter fragments. These factors lead to less recolonizing of small forest patches after they lose species (Butaye et al. 2002, Hanski 2005). The end result is a highly dynamic species composition within small forest patches, as we document here. This dynamism makes evaluations of biodiversity based on a single sampling event unlikely to give an accurate assessment of the status of the species found there, especially for those that are rare. For example, for over half the bird species we documented breeding in HMF we had at best a 50% chance of detecting them when present, with 13 of the 16 species we document as extirpated falling into this category. If we had only one sampling event across less than four years, as is typical for many biodiversity assessments (Raynor et al. 2013), we would have failed to capture the loss of over half of these species and would have substantially overvalued the effectiveness of HMF.

The actions of local governments, not-for-profit organizations, and private citizens have been instrumental in establishing protected areas recently (Dearden et al. 2005). This 'bottom-up' approach to protected area establishment has led to a clear downward shift in protected area size worldwide and a shift toward placing them in urbanizing landscapes (Maiorano et al. 2008). Due to cost constraints, the habitats within these smaller protected areas are also often left unmanaged (Bruner et al. 2004; Paillet et al. 2010). These trends complicate efforts to show the long-term biodiversity benefits of protected areas. The little evidence available (Gaston et al. 2009) may be an unrepresentative sample of the effectiveness of current protected areas. Given this perspective, our results on the long-term effectiveness of a relatively small and unmanaged protected temperate forest provides unique insight into the effectiveness of the many thousands of similar protected areas established in the last two decades.

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References

- Ando A, Camm J, Polasky S, Solow A (1998) Species Distributions, Land Values, and Efficient Conservation. Science 279:2126–2128. doi: <u>10.1126/science.279.5359.2126</u>
- Andrén H (1996) Population Responses to Habitat Fragmentation: Statistical Power and the Random Sample Hypothesis. Oikos 76:235–242. doi: <u>10.2307/3546195</u>
- Aronson MFJ Ecological change by alien plants in an urban landscape. Ph.D. thesis. Rutgers University, New Brunswick, NJ
- Aronson MFJ, Handel SN (2011) Deer and Invasive Plant Species Suppress Forest Herbaceous Communities and Canopy Tree Regeneration. Natural Areas Journal 31:400–407. doi: <u>10.3375/043.031.0410</u>
- Augustine DJ, Jordan PA (1998) Predictors of White-Tailed Deer Grazing Intensity in Fragmented Deciduous Forests. The Journal of Wildlife Management 62:1076–1085. doi: <u>10.2307/3802560</u>
- Baiser B, Lockwood JL, La Puma D, Aronson MFJ (2008) A perfect storm: two ecosystem engineers interact to degrade deciduous forests of New Jersey. Biological Invasions 10:785–795. doi: <u>10.1007/s10530-008-9247-9</u>
- Bartoń K (2018) MuMIn: Multi-Model Inference
- Blake JG, Loiselle BA (2001) Bird Assemblages in Second-Growth and Old-Growth Forests, Costa Rica: Perspectives from Mist Nets and Point Counts. The Auk 118:304–326. doi: <u>10.2307/4089793</u>
- Brown DG, Johnson KM, Loveland TR, Theobald DM (2005) Rural Land-Use Trends in the Conterminous United States, 1950–2000. Ecological Applications 15:1851–1863. doi: <u>10.1890/03-5220</u>
- Bruner AG, Gullison RE, Balmford A (2004) Financial Costs and Shortfalls of Managing and Expanding Protected-Area Systems in Developing Countries. BioScience 54:1119–1126. doi: <u>10.1641/0006-</u> <u>3568(2004)054[1119:FCASOM]2.0.CO;2</u>
- Buell (1957) William L Hutcheson Memorial Forest Bulletin
- Butaye J, Jacquemyn H, Honnay O, et al (2002) The species pool concept applied to forests in a fragmented landscape: dispersal limitation versus habitat limitation. Journal of Vegetation Science 13:27–34. doi: <u>10.1658/1100-9233(2002)013[0027:TSPCAT]2.0.CO;2</u>
- Cameron C, Windmeijer F R-Squared Measures for Count Data Regression Models With Applications to Health-Care Utilization. : Journal of Business & Economic Statistics 14:
- Chape S, Harrison J, Spalding M, Lysenko I (2005) Measuring the extent and effectiveness of protected areas as an indicator for meeting global biodiversity targets. Philosophical Transactions of the Royal Society of London B: Biological Sciences 360:443–455. doi: <u>10.1098/rstb.2004.1592</u>

- Côté SD, Rooney TP, Tremblay J-P, et al (2004) Ecological Impacts of Deer Overabundance. Annual Review of Ecology, Evolution, and Systematics 35:113– 147. doi: <u>10.1146/annurev.ecolsys.35.021103.105725</u>
- Daughtrey ML, Hibben and CR (1994) Dogwood Anthracnose: A New Disease Threatens Two Native Cornus Species. Annual Review of Phytopathology 32:61–73. doi: <u>10.1146/annurev.py.32.090194.000425</u>
- Dauvin J-C (2015) History of benthic research in the English Channel: From general patterns of communities to habitat mosaic description. Journal of Sea Research 100:32–45. doi: <u>10.1016/j.seares.2014.11.005</u>
- Davis MD (1993) Old growth in the East: a survey. Cenozoic Society, Richmond, Vt
- Dearden P, Bennett M, Johnston J (2005) Trends in global protected area governance, 1992-2002. Environ Manage 36:89–100. doi: <u>10.1007/s00267-004-</u> <u>0131-9</u>
- DeFries R, Hansen A, Newton AC, Hansen MC (2005) Increasing Isolation of Protected Areas in Tropical Forests Over the Past Twenty Years. Ecological Applications 15:19–26. doi: 10.1890/03-5258
- Diamond JM (1969) Avifaunal equilibria and species turnover rates on the channel islands of California. Proc Natl Acad Sci U S A 64:57–63
- Edwards AM, Phillips RA, Watkins NW, et al (2007) Revisiting Lévy flight search patterns of wandering albatrosses, bumblebees and deer. Nature 449:1044– 1048. doi: <u>10.1038/nature06199</u>
- Faaborg J, Holmes RT, Anders AD, et al (2010) Conserving migratory land birds in the new world: do we know enough? Ecol Appl 20:398–418
- Fisichelli NA, Abella SR, Peters M, Krist FJ (2014) Climate, trees, pests, and weeds: Change, uncertainty, and biotic stressors in eastern U.S. national park forests. Forest Ecology and Management 327:31–39. doi: 10.1016/j.foreco.2014.04.033
- Fujiwara M, Caswell H (2002) A General Approach to Temporary Emigration in Mark–Recapture Analysis. Ecology 83:3266–3275. doi: <u>10.1890/0012-</u> <u>9658(2002)083[3266:AGATTE]2.0.CO;2</u>
- Gaston KJ, Jackson SF, Cantú-Salazar L, Cruz-Piñón G (2008) The Ecological Performance of Protected Areas. Annual Review of Ecology, Evolution, and Systematics 39:93–113. doi: <u>10.1146/annurev.ecolsys.39.110707.173529</u>
- Geldmann J, Coad L, Barnes M, et al (2015) Changes in protected area management effectiveness over time: A global analysis. Biological Conservation 191:692–699. doi: <u>10.1016/j.biocon.2015.08.029</u>
- Gurd DB, Nudds TD, Rivard DH (2001) Conservation of Mammals in Eastern North American Wildlife Reserves: How Small Is Too Small? Conservation Biology 15:1355–1363. doi: <u>10.1111/j.1523-1739.2001.00188.x</u>

- Hannah L, Midgley G, Andelman S, et al (2007) Protected area needs in a changing climate. Frontiers in Ecology and the Environment 5:131–138. doi: 10.1890/1540-9295(2007)5[131:PANIAC]2.0.CO;2
- Hanski I (2005) Landscape fragmentation, biodiversity loss and the societal response: The longterm consequences of our use of natural resources may be surprising and unpleasant. EMBO reports 6:388–392. doi: <u>10.1038/sj.embor.7400398</u>
- Honnay O, Verheyen K, Hermy M (2002) Permeability of ancient forest edges for weedy plant species invasion. Forest Ecology and Management 161:109–122. doi: <u>10.1016/S0378-1127(01)00490-X</u>
- Iknayan KJ, Tingley MW, Furnas BJ, Beissinger SR (2014) Detecting diversity: emerging methods to estimate species diversity. Trends in Ecology & Evolution 29:97–106. doi: <u>10.1016/j.tree.2013.10.012</u>
- Jokimäki J, Huhta E (2000) Artificial nest predation and abundance of birds along an urban gradient. The Condor 102:838–847. doi: <u>10.1650/0010-</u> <u>5422(2000)102[0838:ANPAAO]2.0.CO;2</u>
- Kéry M, Spillmann JH, Truong C, Holderegger R (2006) How biased are estimates of extinction probability in revisitation studies? Journal of Ecology 94:980–986. doi: <u>10.1111/j.1365-2745.2006.01151.x</u>
- Kissling ML, Garton EO, Handel CM (2006) Estimating detection probability and density from point-count surveys: a combination of distance and doubleobserver sampling. The Auk 123:735–752. doi: <u>10.1642/0004-</u> <u>8038(2006)123[735:EDPADF]2.0.CO;2</u>
- Laurance WF, Carolina Useche D, Rendeiro J, et al (2012) Averting biodiversity collapse in tropical forest protected areas. Nature 489:290–294. doi: 10.1038/nature11318
- Leck CF, Murray BG, Swinebroad J (1988) Long-term changes in the breeding bird populations of a New Jersey forest. Biological Conservation 46:145–157. doi: <u>10.1016/0006-3207(88)90097-3</u>
- Link WA, Sauer JR (1998) Estimating Population Change from Count Data: Application to the North American Breeding Bird Survey. Ecological Applications 8:258–268. doi: <u>10.1890/1051-</u> 0761(1998)008[0258:EPCFCD]2.0.CO;2
- Loss SR, Will T, Marra PP (2013) The impact of free-ranging domestic cats on wildlife of the United States. Nature Communications 4:1396. doi: <u>10.1038/ncomms2380</u>
- Lovett GM, Canham CD, Arthur MA, et al (2006) Forest Ecosystem Responses to Exotic Pests and Pathogens in Eastern North America. BioScience 56:395–405. doi: <u>10.1641/0006-3568(2006)056[0395:FERTEP]2.0.CO;2</u>

- Maiorano L, Falcucci A, Boitani L (2008) Size-dependent resistance of protected areas to land-use change. Proceedings of the Royal Society of London B: Biological Sciences 275:1297–1304. doi: <u>10.1098/rspb.2007.1756</u>
- Meiners SJ (2007) Native and Exotic Plant Species Exhibit Similar Population Dynamics During Succession. Ecology 88:1098–1104. doi: <u>10.1890/06-1505</u>
- Mooney HA, Cleland EE (2001) The evolutionary impact of invasive species. PNAS 98:5446–5451. doi: 10.1073/pnas.091093398
- Oksanen J, Blanchet FG, Friendly M, et al (2017) vegan: Community Ecology Package
- Opdam P (1991) Metapopulation theory and habitat fragmentation: a review of holarctic breeding bird studies. Landscape Ecol 5:93–106. doi: <u>10.1007/BF00124663</u>
- Paillet Y, Bergès L, Hjältén J, et al (2010) Biodiversity Differences between Managed and Unmanaged Forests: Meta-Analysis of Species Richness in Europe. Conservation Biology 24:101–112. doi: <u>10.1111/j.1523-</u> <u>1739.2009.01399.x</u>
- Podani J (1994) Multivariate data analysis in ecology and systematics: a methodological guide to the SYN-TAX 5.0 Package. SPB Academic Publ, The Hague
- Pollock KH (1982) A Capture-Recapture Design Robust to Unequal Probability of Capture. The Journal of Wildlife Management 46:752–757. doi: <u>10.2307/3808568</u>
- Ralph CJ, Geupel GR, Pyle P, et al (1993) Handbook of field methods for monitoring landbirds. U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station, Albany, CA
- Rayner L, Lindenmayer DB, Wood JT, et al (2014) Are protected areas maintaining bird diversity? Ecography 37:43–53. doi: <u>10.1111/j.1600-0587.2013.00388.x</u>
- Robb GN, McDonald RA, Chamberlain DE, et al (2008) Winter feeding of birds increases productivity in the subsequent breeding season. Biology Letters 4:220–223. doi: <u>10.1098/rsbl.2007.0622</u>
- Rodrigues ASL, Akçakaya HR, Andelman SJ, et al (2004) Global Gap Analysis: Priority Regions for Expanding the Global Protected-Area Network. BioScience 54:1092–1100. doi: <u>10.1641/0006-3568(2004)054[1092:GGAPRF]2.0.CO;2</u>
- Roff DA (1973) On the accuracy of some mark-recapture estimators. Oecologia 12:15–34. doi: <u>10.1007/BF00345468</u>
- Schoener TW (1983) Rate of Species Turnover Decreases from Lower to Higher Organisms: A Review of the Data. Oikos 41:372–377. doi: 10.2307/3544095
- Sigel BJ, Douglas Robinson W, Sherry TW (2010) Comparing bird community responses to forest fragmentation in two lowland Central American reserves. Biological Conservation 143:340–350. doi: <u>10.1016/j.biocon.2009.10.020</u>

- Sigel BJ, Sherry TW, Young BE (2006) Avian Community Response to Lowland Tropical Rainforest Isolation: 40 Years of Change at La Selva Biological Station, Costa Rica. Conservation Biology 20:111–121. doi: <u>10.1111/j.1523-</u> <u>1739.2005.00293.x</u>
- Tingley MW, Beissinger SR (2009) Detecting range shifts from historical species occurrences: new perspectives on old data. Trends in Ecology & Evolution 24:625–633. doi: <u>10.1016/j.tree.2009.05.009</u>
- Veall MR, Zimmermann KF (1996) Pseudo-R2 Measures for Some Common Limited Dependent Variable Models. Journal of Economic Surveys 10:241–259. doi: <u>10.1111/j.1467-6419.1996.tb00013.x</u>
- Virkkala R, Pöyry J, Heikkinen RK, et al (2014) Protected areas alleviate climate change effects on northern bird species of conservation concern. Ecology and Evolution 4:2991–3003. doi: <u>10.1002/ece3.1162</u>
- Wang Y, Finch DM (2002) Consistency of Mist Netting and Point Counts in Assessing Landbird Species Richness and Relative Abundance during Migration. The Condor 104:59–72
- Wesołowski T, Czeszczewik D, Hebda G, et al (2015) 40 Years of Breeding Bird Community Dynamics in a Primeval Temperate Forest (Białowieża National Park, Poland). Acta Ornithologica 50:95–120. doi: <u>10.3161/00016454AO2015.50.1.010</u>
- World Conservation Union and UNEP-World Conservation Monitoring Center (2017) World Database on Protected Areas. Version 2017 WCMC. Cambridge, UK

Tables

Table 1. Land cover by year in a 3 km area surrounding Hutcheson MemorialForest. Land classification derived from georectified GIS images. While forestedareas around HMF remain stable, there is a decrease in agricultural land and scrub,and a rise in developed areas.

Landcover	Change in Adjacent (Perimeter) Landcover from 1973-2015	Change in Surrounding 3km area from 1956-2012
Barren	0.56%	1.08%
Agricultural	-58.18%	-32.10%
Developed	0.00%	27.29%
Forest	44.61%	3.05%
Scrub /	13.24%	-8.76%
Wetland		
Water	0.00%	1.94%

Table 2. Weighted averages of the top seven models selected from a GLM that sought to explain changes in species' occupancy rates across time periods. Only models with $\Delta AIC < 2$ were selected for model averaging. A pseudo R² score value of 0.68 was assigned to this model using package modEvA in R 3.3.3.

Effect	Variable	Variable Importanc e	In N significant models	Estimat e	Standar d Error	P Value
Intercept				-0.124	0.102	0.236
BBS		0.53	3	0.042	0.023	0.084.
Regional Trend						
Migratory (Yes)		0.49	3	-0.221	0.101	0.091.
Original		0.15	2	0.0005	0.002	0.841
Size						
Nesting Location		0.07	1			
	Ground			-0.481	0.182	0.011*
	Shrub			-0.239	0.174	0.186
	Tree			-0.228	0.145	0.127

/* *p*< 0.05 / . *p*< 0.

Figures



Figure 1. The upper left map displays New Jersey's relative position in the United States. New Jersey is broken into counties with Somerset County highlighted in dark gray and Hutcheson Memorial forest marked as a small dot on the map. Imagery from Google Earth (2016)



Community Composition of Year

Figure 2. Non-metric multidimensional scaling of bird communities by year. Distance between points represents dissimilarities in the communities. Historic and current communities form two distinct clusters represented by dark gray and light white ellipses respectively. Dots represent bird community composition for the corresponding year. Highest correlation value of 0.91 was obtained when annual composition values were split into current and historical time periods (see text for details)



Figure 3. Predictions derived from breeding bird survey trends in conjunction with population estimates from the historic data are compared with observed populations from recent banding dates. Each dot represents a different species. Horizontal placement of dots is determined by regional growth trends from the BBS with 95% CI. Vertical placement is determined by subtracting the expected number of individuals predicted by BBS trends from the actual number of individuals captured (e.g. BBS trends for Ovenbirds are -0.86 (CI. -1.7,-0.05) and these trends predict a population of 36 individuals (CI. 24,54) but 0 were captured. This places the point for Ovenbirds at -0.86,-36). Species falling along the x-axis as well as in the top right and bottom left of the figure are likely following regional population trends. Species falling in the top left of the graph are persisting at higher numbers despite regionally declining. Species falling in the bottom right of the graph show decline or are increasing at a rate lower than expected given a regionally growing population.



Figure 4. Photos of Hutcheson Memorial Forest (New Jersey, US) in 1973 (left) and 2005 (right) illustrating the loss of understory vegetation over time due to species invasions and deer over-browsing. Photo credits: Jim Quinn (left) and Myla Aronson (right).

Supplemental Material

Table S1: Variable definitions and ranges used in generalized linear mixed-model.

Table S2: Complete list of all species used for analysis. This list includes life history traits of all species as well as historic and current detection probability, change in occupancy between time periods, as well as historic, current, and estimated populations.

Table S1. Variables used in generalized linear mixed-model. Values for categorical variables were gathered from the Cornell

 Lab of Ornithology as was migratory statues. Minimum population size was determined from historical mist netting data.

 Regional growth rate was gathered from the New Jersey specific Breeding Bird Survey information.

Variable	Type of Variable	Range Values	Explanation
Migratory Status	Binary	0 or 1	Represents whether the species is only present during the breeding season (1) or is a yearlong resident of the areas (0)
Nesting Location	Categorical	Cavity, Ground, Shrub, or Tree	Preferred nesting location of a species
Foraging Behavior	Categorical	Foliage gleaning, ground foraging, bark foraging, or flycatching	How the species typically gathers food
Habitat Preference	Categorical	Marsh, Open Woodlands, Forest, Grasslands, Town, or Scrub	Habitat the species is most often found in
Diet	Categorical	Insects, omnivore, or seeds	Primary diet of a species
Initial Minimum Population Size	Continuous	0 to +infinity	Number of unique individuals captured of a given species during the historic period
Regional Growth Rate	Continuous	± infinity	Average yearly population growth rate from the Breeding Bird Survey for a given species in New Jersey

Table S2. All species captured at Hutcheson Memorial Forest (US) in the current and historical time periods. See text for details on derivation of life history and abundance trends. Habitat is preferred habitat type, Food is preferred diet, Nesting is preferred nesting location, Behavior is foraging behavior, Migrant represents whether or not species are seasonal migrants, BBS Trend is the regional growth trend from the New Jersey Breeding Bird Survey (2.4 = growth rate of 1.024), Δ Occupancy is change in occupancy rate from historic to current data, HP is the number of unique individuals captured in the historic period, CP is number of unique individuals captured in the current time period, and BBS Estimates are derived estimates for how many unique individuals we would expect to see given low growth trends, average growth trends, and high growth trends, in that order. These trends represent a 95% confidence interval in growth rates.

Species	Habitat	Food	Nesting	Behavior	Migrant	BBS Trend	Historic p	Current p	∆ Occupancy	HP	СР	BBS Estimate
American Redstart*	forest	insects	tree	FG	yes	2.6	0.13		-0.29	4	0	3716
American Robin	0 W	insects	tree	GF	no	-0.37	0.38	0.43	0.15	58	51	4049 59
Baltimore Oriole	0 W	insects	tree	FG	yes	-3.08	0.31	0.2	-0.43	6	3	357
Black-and- white Warbler*	forest	insects	ground	BF	yes	-2.47	0.13		-0.57	6	0	124
Black-billed Cuckoo*	forest	insects	tree	FG	yes	-2.57	0.15		-0.29	5	0	012
Black- capped Chickadee	forest	insects	cavity	FG	no	0.2	0.27	0.35	0	3	4	247

Blue Jay	forest	omnivore	tree	GF	no	-1.61	0.29	0.46	0	28	28	1013 17
Blue-winged Warbler Brown Creeper*	0 W	insects	ground	FG	yes	-4.91	0.13	0.2	-0.43	3	1	001
	forest	insects	tree	BF	no	1.12	0.13		-0.29	6	0	0237
Brown Thrasher*	scrub	omnivore	shrub	GF	yes	-5.06	0.27		-0.57	20	0	112
Brown- headed Cowbird	grasslan d	seeds	tree	GF	no	1.67	0.16	0.26	-0.14	9	7	1519 41
Carolina Chickadee*	forest	insects	cavity	FG	no	0.09	0.13		-0.14	3	0	134
Carolina Wren Common Grackle Common Yellowthroa t Downy Woodpecker	0 W	insects	cavity	GF	no	6.18	0.21	0.26	0.71	4	11	71740
	0 W	omnivore	tree	GF	no	-3.16	0.25	0.2	-0.43	33	1	5812
	scrub	insects	shrub	FG	yes	-2.8	0.13	0.28	0.57	1	10	000
	O W	insects	cavity	BF	no	0.82	0.23	0.28	-0.14	14	11	1421 32
Eastern Kingbird*	grasslan d	insects	tree	FC	yes	-3.28	0.13		-0.14	3	0	000
Eastern Towhee Eastern Wood- Pewee	scrub	omnivore	ground	GF	yes	0.42	0.3	0.38	0	36	31	123
	forest	insects	tree	FC	yes	-2.63	0.22	0.19	-0.28	6	4	5712
European Starling*	town	insects	cavity	GF	no	-4.33	0.13		-0.29	7	0	001

Gray Catbird	0 W	insects	shrub	GF	no	0.91	0.89	0.92	0	66	19 7	88114 145
Great Crested Flycatcher	O W	insects	cavity	FC	yes	1.13	0.13	0.14	-0.43	9	1	1016 25
Hairy Woodpecker	forest	insects	cavity	BF	no	0.12	0.16	0.3	0.15	4	11	249
House Wren	ΟW	insects	cavity	FG	yes	-0.58	0.16	0.19	0.14	3	4	223
Indigo Bunting	0 W	insects	shrub	FG	yes	-1.29	0.13	0.2	-0.57	7	1	346
Kentucky Warbler*	forest	insects	ground	GF	yes	-4.09	0.13		-0.14	1	0	001
Northern Cardinal	0 W	seeds	shrub	GF	no	2.05	0.22	0.31	0.14	15	18	3038 50
Northern Flicker	0 W	insects	cavity	GF	no	-3.51	0.27	0.2	-0.42	14	3	234
Northern Mockingbird *	town	omnivore	shrub	GF	no	-2.6	0.13		-0.14	2	0	111
Ovenbird*	forest	insects	ground	GF	yes	-0.86	0.41		-1	58	0	2437 54
Red-bellied Woodpecker	forest	insects	cavity	BF	no	6.65	0.13	0.23	0.57	5	14	1929 44
Red-Eyed Vireo*	forest	insects	tree	GF	yes	0.8	0.21		-0.86	15	0	1319 30
Red-winged Blackbird*	marsh	insects	shrub	GF	no	-1.69	0.13		-0.57	11	0	346
Rose- breasted Grosbeak	forest	insects	tree	FG	yes	-3.54	0.16	0.19	0.14	7	7	113
Scarlet Tanager	forest	insects	tree	FG	yes	0.78	0.26	0.2	-0.42	20	2	1730 53

Song Sparrow*	O W	insects	shrub	GF	no	-2.09	0.14		-0.71	9	0	233
Tufted Titmouse	forest	insects	cavity	FG	no	1.88	0.13	0.23	-0.18	14	9	2334 49
Veery*	forest	insects	ground	GF	yes	-0.82	0.16		-0.78	5	0	135
White- Breasted Nuthatch	forest	insects	cavity	BF	no	3.56	0.15	0.23	-0.18	5	7	1325 47
Wood Thrush	forest	insects	tree	GF	yes	-1.59	0.57	0.61	0	132	49	4561 86
Yellow-billed Cuckoo*	O W	insects	tree	FG	yes	0.31	0.13		-0.43	7	0	158

OW = Open Woodlands FG = foliage gleaning, GF = ground foraging, BF = bark foraging FC = flycatching.

* represents species not present in the current data

Protected forests provide varied biodiversity experiences within an urban

landscape

Abstract

Over 60% of the world's population lives in urban areas and this number is predicted to increase to nearly 70% in the next 30 years. Individuals living within urban areas often lack access to nature and the associated health and psychological benefits natural areas provide. Recent research shows that visitors to natural areas that are relatively species rich report increased health and sense of well-being (cultural ecosystem services), even though these visitors were unable to differentiate between areas of low and high species richness. Understanding this so-called 'peoplebiodiversity paradox' requires moving beyond the traditional view that higher species richness leads to more rewarding experience in nature. Instead, recognizing that urban residents may be responding to different elements of biodiversity and the full range of experiences natural areas can provide. Here, we review evidence that people value a variety of biodiversity facets beyond richness, including uniqueness and rarity. We then measure four aspects of avian diversity within and across 60 urban protected forests in New Jersey (USA) evaluating the extent to which these metrics co-vary within the same forest, and across forests. We found that, for any single protected forest, species richness does not adequately capture variation in rarity or uniqueness. We also show that all four biodiversity metrics vary widely across forests in response to surrounding land uses and forest size. Our results demonstrate that in addition to acknowledging the intricacies of humans' perceptions of biodiversity, the burgeoning study of cultural ecosystem services must explicitly consider the complexity in biodiversity metrics and how these metrics differ across urban natural areas.

Introduction

By 2050 nearly 70% of the world's population will live in urban areas (United Nations Department of Economic and Social Affairs, 2018), resulting in an at least 15.5 million km² of land being converted for urban land uses (Seto, Güneralp, & Hutyra, 2012). As urbanization increases, many people lose access to nature, resulting in a decrease in their physical and mental health (Chiesura, 2004; Gilbert & Phillips, 2003; Nielsen & Hansen, 2007). One solution to this dilemma is for urban planners to protect natural habitat as open spaces allowing urban residents easy and direct interactions with the living world (Jennings, Johnson Gaither, & Gragg, 2012). Although evidence that access to these protected spaces provides positive benefits is mounting, the mechanisms by which these benefits are achieved remains unclear (Barton & Pretty, 2010; Driver, Rosenthal, & Peterson, 1980; Shanahan et al., 2016; Shanahan, Fuller, Bush, Lin, & Gaston, 2015). An intriguing connection posits that benefits of protected natural areas are tied to the biodiversity of those spaces where, as richness increases, so do benefits (Cox & Gaston, 2015; Dallimer et al., 2012; Devictor et al., 2010; Hoyle, 2015; Sandifer, Sutton-Grier, & Ward, 2015). However, there remain large uncertainties surrounding this connection including evidence that people cannot discern differences in species richness between sites themselves (Pett, Shwartz, Irvine, Dallimer, & Davies, 2016; Shwartz, Turbé, Simon, & Julliard, 2014). This so-called 'people-biodiversity paradox' reflects the varied dimensions through which people perceive and respond to natural environments, and how these responses are themselves determined by individual cultural, economic, and experiential backgrounds (Shwartz et al., 2014). There has been surprisingly little exploration, however, of the multi-dimensionality of the

biodiversity side of this paradox, leaving a significant gap in our ability to 'unpick' the paradoxical knot that ties human health and species richness (Pett et al., 2016).

Most research effort on the people-biodiversity paradox has measured biodiversity as simple tallies of species present (i.e., species richness), or in terms of the presence of broad functional groups (e.g., cavity nesting birds or colorful flowers; Cox & Gaston, 2015; Dallimer et al., 2012). These biodiversity metrics, while relatively easy to measure, do not adequately reflect current knowledge of how species respond to urban landscapes as they often miss changes in species identity and spatial turnover in community composition (Angold et al., 2006; Lovell, Wheeler, Higgins, Irvine, & Depledge, 2014). Urban and urbanizing landscapes have complex and heterogenous land-use patterns (Taylor, 2016), resulting in equally varied patterns in biodiversity (Honnay, Verheyen, & Hermy, 2002; Williams, Morgan, Mcdonnell, & Mccarthy, 2005; Woodroffe & Ginsberg, 1998). For example, larger patches of urban open space tend to support species that require relatively large home ranges, are sensitive to subtle habitat differences within the site (i.e., edge effects), or utilize a range of resources that can only be found in larger habitat patches (Godefroid & Koedam, 2003; Harrison & Bruna, 1999; Hodgson, Moilanen, Wintle, & Thomas, 2011). As a result, small urban natural areas may be depauperate of species that are dependent on specific habitat types (forest, wetland) or that are of regional conservation concern (Knapp, Kühn, Mosbrugger, & Klotz, 2008; Mcdonald et al., 2009). Similarly, land-uses surrounding urban open space have a strong influence on the species found within (Diekötter, Haynes, Mazeffa, & Crist, 2007; Ockinger, Lindborg, Sjödin, & Bommarco, 2012; Prevedello & Vieira, 2010). Thus, due to the tension between habitat type within the reserve and the

surrounding land use matrix, a protected open space may hold many species (high species richness) that are also found in surrounding landscapes (low uniqueness). If people are responding to these aspects of urban biodiversity more than richness alone, then the failure to account for the complex response of species to urban landscapes can help explain the people-biodiversity paradox (Table 1; Church et al. 2014; Graves, Pearson, & Turner, 2017).

Recent research suggests that people respond to nature in ways that link to both species' rarity and uniqueness (Dunn et al. 2006; Louv 2008; Johnson et al. 2010, Fairchild et al. 2018). For example, Palliwoda et al. (2017) found that the presence of species within the natural area that are not in surrounding developed landscapes (uniqueness) was critical to the magnitude of the benefit people received from visiting natural areas. Similarly, both urban foragers and bird watchers, two large and growing urban populations, show strong connections to species identity and likely perceive the value of an area in terms of whether key habitat-specific species are present as opposed to responding to total species richness (Cox & Gaston, 2015; Poe, LeCompte, McLain, & Hurley, 2014). Finally, Angulo et al. (2009) provide experimental evidence that people place very high value on interacting with rare species often enduring physical hardship or spending extra time to see them. Birds, in particular, provide many important cultural services (Wenny, Devault, & Johnson, 2011; Whelan, Wenny, & Marquis, 2008), including representing "...a relatable component of the broader environment to which people can develop attachments" (Belaire, Westphal, Whelan, & Minor, 2015), and they are our focal group here.

We explored several aspects of avian biodiversity within urban forested protected areas within the New Jersey Highlands (USA). Approximately 850,000 people live within the Highlands at densities ranging from 50 to >2,500 individuals per square kilometer (US Census 2010). The resulting landscape is a diverse mixture of urban, agricultural, and natural forested areas, and contains over 3,500 protected patches forest that range in size from 5 to >3,000ha (Fenn et al. In Review). These protected forest provide nearby residents with opportunities to directly experience and benefit from forested lands, with 20 million estimated visitors to these sites per year (NJ DEP 2011). Following evidence of how people value and respond to biodiversity (above), we measured for each forested protected area the (1) total bird species (richness), (2) number of species that are dependent on forested habitat (3) number of species that are regionally rare or of conservation concern, and (4) uniqueness of the bird community within the protected area relative to the community in surrounding unprotected habitat.

Methods

Protected Forests

The New Jersey Highlands is a 600,000 ha geographic region in the northeastern United States, which is primarily forested (Lathrop et al. 2007; USGS 2017). Over the past 40 years, the region has experienced a growth in population of ~6% per decade (US Census 2010) leaving a highly heterogenous mixture of land uses (Lathrop, Tulloch, & Hatfield, 2007). For our analysis we selected 60 patches of forest habitat that are included within protected open space designations (hereafter, protected forests) that ranged in size from 10 to 150ha. All 60 sites have been classified as forested land cover over the last 40 years and currently have substantial understory vegetation (Nudds, 1977). We also ensured that all protected forests had a relatively uniform rectangular shape thus maintaining between them a consistent ratio between edge and core habitat.

Using 2012 land-use, land-cover (LULC) data, we classified all land parcels within a 150m buffer around each protected forest as either forested, agricultural, or urban (NJDEP 2012). Using the methodology of Fenn et al. (In Review), we then classified protected forest buffer as 'urban matrix habitat' or 'agricultural matrix habitat' if at least 75% of the surrounding land parcels had LULC urban or agriculture classifications respectively. We classified protected forests as having 'natural matrix habitat' if 75% or more of surrounding land parcels were not protected but still had LULC forest classification. We choose a 150m buffer for all classifications to reflect the average foraging ranges and dispersal distances of the bird species we regularly observed breeding in the protected forests (Blake & Karr, 1987; Grubb & Doherty, 1999).

Bird Sampling

To measure avian use of these protected forests, we conducted point counts within each and within their surrounding matrix habitat. All point counts were fiveminutes duration (Gates 1969), where observers recorded all individual birds seen or heard within 50m of the count location. During each sampling day, we conducted three point counts within each protected forest and within matrix habitat surrounding each forest. The point counts were spaced at least 150m apart and 75m from the forest edge, which ensures that each sample is an independent observation of bird diversity. All protected forests and surrounding matrix habitat were visited a total of four times within the breeding bird season over the course of the study (May 23rd until August 2nd, 2016). All point counts occurred during heightened daily times of bird activity (between 5am and 11am), and counts only occurred on days without rain and when wind was below 15 mph to ensure normal bird activity (Ralph, Geupel, Pyle, Martin, & DeSante, 1993). No new species were observed after sampling day 55 indicating that our sampling effort adequately capture each sites' biodiversity (Supplemental Figure 2).

Biodiversity Metrics

We calculated four biodiversity metrics for each protected forest and surrounding matrix habitat; (1) total species richness (2) richness of forest dependent species (3) richness of species of conservation concern, and (4) compositional similarity between the protected forest and its surrounding matrix habitat (uniqueness; Figure 1).

We estimated species richness for each protected forest, and its surrounding matrix habitat, by averaging the number of species observed in each of the four sampling events conducted per site. We used information within the Cornell Lab of Ornithology Birds of North America (allaboutbirds.org) to classify which of these observed species could be considered forest dependent. We used information from Partners in Flight and the International Union for the Conservation of Nature (IUCN) to identify which of these species are considered threatened with regional or global extinction (Partners in Flight 2017, IUCN 2018). We used the United States Geological Survey (USGS) annual Breeding Bird Survey (BBS, Sauer et al., 2017) to identify which of these observed species showed negative regional population trends over the past 10 years. We refer to all species that were either considered threatened with extinction, or had experienced regional population decline, as 'conservation concern'. We tested whether average species richness, number of forest dependent species, and the number of species of conservation concern differed between protected forests and their surrounding matrix habitats using ANOVA with Tukey's Honest Significant Difference Test (R version 3.3.3; Chambers et al., 1992; Yandell, 1997). We used linear regressions to explore how the four biodiversity metrics varied in association with protected forest size, with the expectation that each metric should increase as size increased. We further evaluated how this relationship varied according to the matrix habitat that surrounding each protected forest (urban, agriculture, natural). We compared the difference between the fit of these regressions using ANOVA (R core team).

Finally, we compared bird species composition within protected forests to their surrounding matrix habitats as a measure of the uniqueness of the experience each protected forest provides visitors. We did this in two ways. First, we calculated the difference in the above biodiversity metrics between each protected forest and its surrounding matrix habitat, and evaluated whether matrix habitat type (urban, agriculture, natural) influenced the magnitude of these differences using ANOVA. Second, we created Bray-Curtis species composition dissimilarity for each protected forest and its surrounding matrix habitat using presence-absence information from the point counts. We portrayed compositional dissimilarity in twodimensional space using non-metric multi-dimensional scaling (NMDS, package vegan in R version 3.3.3; Oksanen et al., 2018). Within this two-dimensional space, the Euclidian distance between any two points represents the degree of dissimilarity in species composition between the two sites these points represent. We matched each protected forest to its matrix habitat, and measured the Euclidian distance between these two points in the NMDS two-dimensional space (see Supplemental Figure 1). Longer distances between a protected forest and its matrix habitat indicates increased dissimilarity in species composition between them, and vice versa. We used linear regressions to determine the relationship between protected forest size and how dissimilar its species composition was from that of its surrounding matrix habitat. We repeated this regression across each matrix type (urban, agriculture and natural) and compared the slopes of these regressions using ANOVA.

Results

Of the 60 protected forests, we classified 19 as having agricultural, 21 urban, and 20 natural matrix habitat. The average size of all forests was 33.85ha (SD = 35.26) with no difference in forest size between matrix habitat types (n = 60, p = 0.29, df = 2). We recorded a total of 5,935 individual birds representing 79 species with an average of 17.8 (SD =5.71) species found within protected forests.

Of the 63 species we observed within protected forests, 23 were considered forest dependent. Only 7 of these species were observed exclusively within protected forest (e.g., Acadian flycatcher, *Empidonax virescens*, black-and-white warbler, *Mniotilta varia*, and pileated woodpecker, *Dryocopus pileatus*), while the other 16 were observed in protected forests and surrounding matrix habitat. Only one species, the wood thrush (*Hylocichla mustelina*), was listed as threatened with regional or global extinction, however 16 species exhibited regional population declines (including wood thrush). We observed 71 species across all matrix habitat types, with 14 found exclusively within matrix habitats and not within protected forests. Many of these matrix-only species were grassland specialists observed within agricultural matrix habitat (e.g., grasshopper sparrow, *Ammodramus* savannarum, eastern meadowlark, *Sturnella magna*, and barn swallow, *Hirundo rustica*). Of the species found in matrix habitat, 5 were considered threatened with regional or global extinction (e.g. bobolink, *Dolichonyx oryzivorus*, and grasshopper sparrow, *Ammodramus savannarum*) and 27 showed regional population declines.

We found that protected forests surrounded by urban matrix habitat on average held four fewer species than protected forests surrounded by agricultural habitat (average 14.8 and 18.7 species respectively; Table 2). Protected forests surrounded by urban matrix habitat also contained two fewer forest dependent species on average than protected forests surrounded by natural habitat matrix (average 6.76 and 8.69 species respectively; Table 2). We found that the number of species of conservation concern was the same across protected forests (average of 4.05) regardless of their surrounding matrix habitat types (Table 2).

We found that protected forests surrounded by natural matrix habitat held an average of 4.11 more forest dependent species than forests surrounded by agricultural matrix habitat, and 3.53 more than in forests surrounded by urban matrix habitat (Table 3). When protected forests were surrounded by urban matrix habitat, the urban matrix held 2.33 more species than the protected forests (Table 3). Finally, we found that agricultural matrix habitat had on average 3.84 more species of conservation concern than the protected forests they surrounded. There were no other differences in numbers of species of conservation concern between a protected forest and its matrix habitat.

When incorporating the influence of the size of protected forest on bird diversity, we observed unique trends across protected forests surrounded by the three matrix habitat types. We observed no significant rise in species richness as the size of the protected forest increased if it was surrounded by agricultural and natural matrix habitats. However, we observed a significant decrease (-0.04 species/ha. p<0.05) in species richness as the size of protected forests increased if they were surrounded by urban matrix habitats (Figure 2A). We observed no relationship between protected forest size and the number of forest dependent species it contained if it was surrounding by natural matrix habitat. There was a significant increase in the number of forest dependent species as protected forest size increased if the forest was surrounded by agricultural and urban matrix habitats (0.05 species/ha. p<0.03 and 0.03 species/ha. p<0.01, Figure 2C). This increase in forest dependent species likely contributed to the significantly increasing compositional dissimilarity seen in forests surrounded by urban and agricultural matrix habitats (p<0.01, p<0.02, Figure 2B). The number of species of conservation concern did not vary across protected forest size regardless of matrix habitat (Figure 2D). In total, these results show that a single protected forest can present divergent biodiversity metrics such that a forest that has high values in one metric may have low values for another (e.g., red highlighted protected forest in Figure 2).

The Euclidean distance between protected forests and their surrounding matrix habitat averaged 0.562 (SD 0.28) and ranged from 0.096 (forest very similarly in composition to its matrix) to 1.468 (forest very dissimilar to its matrix). In the former case, of 19 total species observed in the protected forest, 12 were also found in the matrix habitat and 5 were found in the matrix habitat but not the forest. In the latter case, we observed 10 species within the protected forest, 2 of which were also found in the surrounding matrix habitat and a 14 additional species were found in the matrix but not in the forest. Average species dissimilarity was the highest between protected forests and their agricultural matrix habitat (0.686, SD 0.27; Table 3) and lowest between protected forests and their corresponding natural matrix habitat (0.397, SD 0.17; Table 3). These similarity scores were statistically different from the overall dissimilarity (p < 0.05 and p < 0.01). In general, patterns of dissimilarity between a protected forest and its matrix habitat were driven by the presence or absence of forest dependent birds. While these species were sometimes observed outside of protected forests, especially within urban matrix habitat, they were rarely seen in agricultural matrix habitat. Conversely, grassland species that were common in agricultural matrix habitat were rare within protected forests resulting in increased dissimilarity.

Discussion

As the number of people occupying urban centers increases in the coming decades, cities will continue to sprawl into natural habitats threatening species and constructing more barriers between people that inhabit urban spaces and the natural landscape (Mcdonald et al., 2009). The threat to biodiversity is exacerbated because many of the most biodiverse regions of the world overlap current and future mega-cities (Brooks et al., 2002; Cincotta, Wisnewski, & Engelman, 2000; Mittermeier, Myers, Thomsen, Da Fonseca, & Olivieri, 1998; Seto et al., 2012). Thus, establishment of protected areas within high human density settings lays the foundation for a win-win outcome whereby habitat loss is reduced and people enjoy better health and a higher sense of well-being (Anguluri & Narayanan, 2017; Takano, Nakamura, & Watanabe, 2002; Wolch, Byrne, & Newell, 2014). To realize these outcomes, however, we require a much better understanding of how biodiversity within protected natural areas varies across urban landscapes, especially in regards the many facets of biodiversity that people value.

Our results highlight the role of protected area size and surrounding land use on the biodiversity they contain. Contrary to our expectations, and those set by traditional species-area relationships (Cain, 1938), we found that avian species richness was higher in smaller protected forests relative to larger forests. While urban habitats are high in species richness, many of these species are urban exploiters (Blair, 1999). While these species drive up richness, they do little to increase the uniqueness of the habitats they occupy (Kark et al. 2007). However, as size of the protected forest increased, the number of species penetrating a protected forest from its surrounding matrix habitat decreased. This shift resulted in a decrease in richness but an increase in the uniqueness of species composition. This increase was further bolstered by species that require larger patches of core habitat persisting within the protected forest. The extent to which this shift in community composition occurred depended on the surrounding matrix type. Urban exploiters were common in both urban landscapes and small urban forests, so protected forests only became dissimilar to their surrounding matrix habitat at larger forest sizes. In contrast, grassland birds that were common in agricultural habitats were uncommon even in small protected forest patches resulting in communities that are dissimilar. Collectively, our results suggest that urban protected areas provided distinctly different 'nature doses' depending on their size and landscape configuration (Schroeder, 1996; Shanahan et al., 2016, 2015).

Further, our results demonstrate larger areas provide urban residents a unique view of nature that is atypical of the surrounding area. While small forests present a rich suite of species, our results indicate that many visitors would be able to see these same species in their own back yard. In contrast, larger protected forests contained fewer species, but those that were in that forest were often forest specialists that could only be experienced within these protected spaces. This contrast in experience likely plays a key role in how visitors perceive these areas as many people visit natural areas 'to see nature' where nature is considered something distinct from what they experience every day (Vinning, Merrick, & Price 2008; Lin et al. 2014). If we focus only on richness when assessing the cultural benefits an open space may provide, we undervalue many areas that provide urban residents the opportunity to experience 'nature' they may otherwise never see (Lindo 2015).

Finally, these results show that avian species richness rarely scales cleanly with other biodiversity metrics within the urban protected forests. We found that, depending on the biodiversity metric considered, a single protected forest may present contradictory biodiversity scores. This result calls for further study using this, or other, urban landscapes to address how people value these different forests. Using citizen scientists and information from social media may provide a reliable way to assess how visitors to these forests are interacting with the biodiversity they present (Tenkanen et al. 2017). Photographs associated with specific open spaces may provide insight into what people value in those areas (Beckley et al. 2005). Matching self-reported values with known biodiversity metrics will give a better understanding of the link between biodiversity and human wellness.

Our work adds to a small, but growing literature on the pitfalls of evaluating the cultural and ecological value of urban protected areas based on simple biodiversity metrics (e.g., Graves et al., 2017). The biodiversity people experience by
visiting urban protected areas is highly dependent on the site they choose, and the facets of biodiversity they value may be absent from sites considered diverse if they are ranked by species richness alone. Thus 'unpicking' the people-biodiversity paradox requires multi-faceted measurements of urban biodiversity with explicit assessment of how these metrics influence provisioning of cultural ecosystem services (Pett et al., 2016; Shwartz et al., 2014). If urban planners take the richnessbased approach to assessing ecosystem services or conservation value, they may ignore biodiversity elements that provide humans with unique experiences or protect species of conservation concern. Furthermore, if planners consider only the size of a habitat patch as an indication of its value and fail to consider its landscape configuration and surrounding matrix, the chance of wasting money and political capital is high. Even large protected areas can provide low cultural services if the services are linked to species identity or the ability of a protected area to provide a unique experience to visitors. A stronger inter-disciplinary approach to both the evaluation and creation of open spaces is well-warranted, including having ecologists and urban planners work together to create conservation and human health win-win outcomes.

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References

United Nations Department of Economic and Social Affairs. (2018). *Revision of World Urbanization Prospects*. Retrieved from https://www.un.org/development/desa/publications/2018-revision-of-worldurbanization-prospects.html

Angold, P. G., Sadler, J. P., Hill, M. O., Pullin, A., Rushton, S., Austin, K., ... Thompson, K. (2006). Biodiversity in urban habitat patches. Science of The Total Environment, 360(1), 196–204. https://doi.org/10.1016/j.scitotenv.2005.08.035

Angulo Elena, Deves Anne-Laure, Saint Jalmes Michel, & Courchamp Franck. (2009). Fatal attraction: rare species in the spotlight. Proceedings of the Royal Society B: Biological Sciences, 276(1660), 1331–1337. https://doi.org/10.1098/rspb.2008.1475

Anguluri, R., & Narayanan, P. (2017). Role of green space in urban planning: Outlook towards smart cities. Urban Forestry & Urban Greening, 25, 58–65. https://doi.org/10.1016/j.ufug.2017.04.007

Barton, J., & Pretty, J. (2010, March 25). What is the Best Dose of Nature and Green Exercise for Improving Mental Health? A Multi-Study Analysis [research-article]. https://doi.org/10.1021/es903183r

Belaire, J. A., Westphal, L. ., Whelan, C. J., & Minor, E. S. (2015). Urabn residents' perceptions of birds in the neighborhood: Biodiversity, cultural ecosystem services, and disservices.

- Blair, R. B. (1999). Birds and Butterflies Along an Urban Gradient: Surrogate Taxa for Assessing Biodiversity? *Ecological Applications*, *9*(1), 164–170. https://doi.org/10.1890/1051-0761(1999)009[0164:BABAAU]2.0.CO;2
- Blake, J. G., & Karr, J. R. (1987). Breeding Birds of Isolated Woodlots: Area and Habitat Relationships. *Ecology*, 68(6), 1724–1734. https://doi.org/10.2307/1939864
- Brooks, T. M., Mittermeier, R. A., Mittermeier, C. G., Fonseca, G. A. B. D., Rylands, A. B., Konstant, W. R., ... Hilton-Taylor, C. (n.d.). Habitat Loss and Extinction in the Hotspots of Biodiversity. *Conservation Biology*, 16(4), 909– 923. https://doi.org/10.1046/j.1523-1739.2002.00530.x
- Cain, S. A. (1938). The Species-Area Curve. The American Midland Naturalist, 19(3), 573–581. https://doi.org/10.2307/2420468
- Chiesura, A. (2004). The role of urban parks for the sustainable city. Landscape and Urban Planning, 68(1), 129–138. https://doi.org/10.1016/j.landurbplan.2003.08.003
- Cincotta, R. P., Wisnewski, J., & Engelman, R. (2000). Human population in the biodiversity hotspots. *Nature*, 404(6781), 990–992. https://doi.org/10.1038/35010105
- Cox, D. T. C., & Gaston, K. J. (2015). Likeability of Garden Birds: Importance of Species Knowledge & Richness in Connecting People to Nature. *PLOS ONE*, 10(11), e0141505. https://doi.org/10.1371/journal.pone.0141505

Dallimer, M., Irvine, K. N., Skinner, A. M. J., Davies, Z. G., Rouquette, J. R., Maltby, L. L., ... Gaston, K. J. (2012). Biodiversity and the Feel-Good Factor: Understanding Associations between Self-Reported Human Well-being and Species Richness. *BioScience*, 62(1), 47–55. https://doi.org/10.1525/bio.2012.62.1.9

- Devictor, V., Mouillot, D., Meynard, C., Jiguet, F., Thuiller, W., & Mouquet, N. (2010). Spatial mismatch and congruence between taxonomic, phylogenetic and functional diversity: the need for integrative conservation strategies in a changing world. *Ecology Letters*, 13(8), 1030–1040. https://doi.org/10.1111/j.1461-0248.2010.01493.x
- Diekötter, T., Haynes, K. J., Mazeffa, D., & Crist, T. O. (2007). Direct and indirect effects of habitat area and matrix composition on species interactions among flower-visiting insects. *Oikos*, *116*(9), 1588–1598. https://doi.org/10.1111/j.0030-1299.2007.15963.x
- Driver, B. L., Rosenthal, D., & Peterson, G. (1980). Social benefits of urban forests and related green spaces in cities. *Proceedings of the National Urban Forestry Conference November 13-16, 1978, Washington, D.C.*, 98–113.
- Gilbert, L., & Phillips, C. (2003). Practices of Urban Environmental Citizenships: Rights to the City and Rights to Nature in Toronto. *Citizenship Studies*, 7(3), 313–330. https://doi.org/10.1080/1362102032000098896
- Godefroid, S., & Koedam, N. (2003). How important are large vs. small forest remnants for the conservation of the woodland flora in an urban context? *Global Ecology and Biogeography*, 12(4), 287–298. https://doi.org/10.1046/j.1466-822X.2003.00035.x
- Graves, R. A., Pearson, S. M., & Turner, M. G. (2017). Landscape dynamics of floral resources affect the supply of a biodiversity-dependent cultural ecosystem service. *Landscape Ecology*, *32*(2), 415–428. https://doi.org/10.1007/s10980-016-0452-0
- Grubb, T. C., & Doherty, P. F. (1999). On Home-Range Gap-Crossing. *The Auk*, 116(3), 618–628. https://doi.org/10.2307/4089323
- Harrison, S., & Bruna, E. (1999). Habitat fragmentation and large-scale conservation: what do we know for sure? *Ecography*, *22*(3), 225–232. https://doi.org/10.1111/j.1600-0587.1999.tb00496.x
- Hodgson, J. A., Moilanen, A., Wintle, B. A., & Thomas, C. D. (2011). Habitat area, quality and connectivity: striking the balance for efficient conservation. *Journal of Applied Ecology*, 48(1), 148–152. https://doi.org/10.1111/j.1365-2664.2010.01919.x
- Honnay, O., Verheyen, K., & Hermy, M. (2002). Permeability of ancient forest edges for weedy plant species invasion. *Forest Ecology and Management*, 161(1), 109–122. https://doi.org/10.1016/S0378-1127(01)00490-X
- Hoyle, H. E. (2015). Human happiness versus urban biodiversity? Public perception of designed urban planting in a warming climate (phd). University of Sheffield. Retrieved from http://etheses.whiterose.ac.uk/10738/?utm_term=wreo&utm_source=twitterfe ed&utm_medium=twitter
- J R Sauer, D K Niven, Hines, J. E., Ziolkowski Jr D, J., K L Pardieck, Fallon, J. E., & Link, W. A. (2017). The North American Breeding Bird Survey, Results and Analysis 1966 - 2015.
- Jennings, V., Johnson Gaither, C., & Gragg, R. S. (2012). Promoting Environmental Justice Through Urban Green Space Access: A Synopsis. *Environmental* Justice, 5(1), 1–7. https://doi.org/10.1089/env.2011.0007

- Knapp, S., Kühn, I., Mosbrugger, V., & Klotz, S. (2008). Do protected areas in urban and rural landscapes differ in species diversity? *Biodiversity and Conservation*, 17(7), 1595–1612. https://doi.org/10.1007/s10531-008-9369-5
- Lathrop, R. G., Tulloch, D. L., & Hatfield, C. (2007). Consequences of land use change in the New York–New Jersey Highlands, USA: Landscape indicators of forest and watershed integrity. *Landscape and Urban Planning*, 79(2), 150–159. https://doi.org/10.1016/j.landurbplan.2006.02.008
- Lovell, R., Wheeler, B. W., Higgins, S. L., Irvine, K. N., & Depledge, M. H. (2014). A Systematic Review of the Health and Well-Being Benefits of Biodiverse Environments. *Journal of Toxicology and Environmental Health, Part B*, 17(1), 1–20. https://doi.org/10.1080/10937404.2013.856361
- Mcdonald, R. I., Forman, R. T. T., Kareiva, P., Neugarten, R., Salzer, D., & Fisher, J. (2009). Urban effects, distance, and protected areas in an urbanizing world. Landscape and Urban Planning, 93(1), 63–75. https://doi.org/10.1016/j.landurbplan.2009.06.002
- Mittermeier, R. A., Myers, N., Thomsen, J. B., Da Fonseca, G. A. B., & Olivieri, S. (1998). Biodiversity Hotspots and Major Tropical Wilderness Areas: Approaches to Setting Conservation Priorities. *Conservation Biology*, *12*(3), 516–520. https://doi.org/10.1046/j.1523-1739.1998.012003516.x
- Nielsen, T. S., & Hansen, K. B. (2007). Do green areas affect health? Results from a Danish survey on the use of green areas and health indicators. *Health & Place*, *13*(4), 839–850. https://doi.org/10.1016/j.healthplace.2007.02.001
- Nudds, T. D. (1977). Quantifying the Vegetative Structure of Wildlife Cover. Wildlife Society Bulletin (1973-2006), 5(3), 113–117.
- Öckinger, E., Lindborg, R., Sjödin, N. E., & Bommarco, R. (2012). Landscape matrix modifies richness of plants and insects in grassland fragments. *Ecography*, 35(3), 259–267. https://doi.org/10.1111/j.1600-0587.2011.06870.x
- Oksanen, J., Blanchet, F. G., Friendly, M., Kindt, R., Legendre, P., McGlinn, D., ... Wagner, H. (2018). vegan: Community Ecology Package (Version 2.5-3). Retrieved from https://CRAN.R-project.org/package=vegan
- Palliwoda, J., Kowarik, I., & von der Lippe, M. (2017). Human-biodiversity interactions in urban parks: The species level matters. *Landscape and Urban Planning*, 157, 394–406. https://doi.org/10.1016/j.landurbplan.2016.09.003
- Pett, T. J., Shwartz, A., Irvine, K. N., Dallimer, M., & Davies, Z. G. (2016). Unpacking the People–Biodiversity Paradox: A Conceptual Framework. *BioScience*, 66(7), 576–583. https://doi.org/10.1093/biosci/biw036
- Poe, M. R., LeCompte, J., McLain, R., & Hurley, P. (2014). Urban foraging and the relational ecologies of belonging. *Social & Cultural Geography*, 15(8), 901– 919. https://doi.org/10.1080/14649365.2014.908232
- Prevedello, J. A., & Vieira, M. V. (2010). Does the type of matrix matter? A quantitative review of the evidence. *Biodiversity and Conservation*, 19(5), 1205–1223. https://doi.org/10.1007/s10531-009-9750-z
- Ralph, C. J., Geupel, G. R., Pyle, P., Martin, T. E., & DeSante, D. F. (1993).
 Handbook of field methods for monitoring landbirds (No. PSW-GTR-144).
 Albany, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Research Station. https://doi.org/10.2737/PSW-GTR-144
- Sandifer, P. A., Sutton-Grier, A. E., & Ward, B. P. (2015). Exploring connections among nature, biodiversity, ecosystem services, and human health and well-

being: Opportunities to enhance health and biodiversity conservation. Ecosystem Services, 12, 1–15. https://doi.org/10.1016/j.ecoser.2014.12.007

- Schroeder, H. W. (1996). Ecology of the Heart: Understanding How People Experience Natural Environments. Retrieved from https://www.nrs.fs.fed.us/pubs/3263
- Seto, K. C., Güneralp, B., & Hutyra, L. R. (2012). Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National Academy of Sciences*, 109(40), 16083–16088. https://doi.org/10.1073/pnas.1211658109
- Shanahan, D. F., Bush, R., Gaston, K. J., Lin, B. B., Dean, J., Barber, E., & Fuller, R. A. (2016). Health Benefits from Nature Experiences Depend on Dose. *Scientific Reports*, 6, 28551. https://doi.org/10.1038/srep28551
- Shanahan, D. F., Fuller, R. A., Bush, R., Lin, B. B., & Gaston, K. J. (2015). The Health Benefits of Urban Nature: How Much Do We Need? *BioScience*, 65(5), 476–485. https://doi.org/10.1093/biosci/biv032
- Shwartz, A., Turbé, A., Simon, L., & Julliard, R. (2014). Enhancing urban biodiversity and its influence on city-dwellers: An experiment. *Biological Conservation*, 171, 82–90. https://doi.org/10.1016/j.biocon.2014.01.009
- Takano, T., Nakamura, K., & Watanabe, M. (2002). Urban residential environments and senior citizens' longevity in megacity areas: the importance of walkable green spaces. *Journal of Epidemiology & Community Health*, 56(12), 913– 918. https://doi.org/10.1136/jech.56.12.913
- Taylor, K. (2016). The Historic Urban Landscape paradigm and cities as cultural landscapes. Challenging orthodoxy in urban conservation. *Landscape Research*, 41(4), 471–480. https://doi.org/10.1080/01426397.2016.1156066
- Wenny, D. G., Devault, T. L., & Johnson, M. D. (2011, June 1). Auk.: The need to quantify ecosystem services provided by birds. Retrieved February 26, 2019, from

http://link.galegroup.com/apps/doc/A262691257/AONE?sid=googlescholar

- Whelan, C. J., Wenny, D. G., & Marquis, R. J. (2008). Ecosystem services provided by birds. Annals of the New York Academy of Sciences, 1134, 25–60. https://doi.org/10.1196/annals.1439.003
- Williams, N. S. G., Morgan, J. W., Mcdonnell, M. J., & Mccarthy, M. A. (2005). Plant traits and local extinctions in natural grasslands along an urban–rural gradient. *Journal of Ecology*, 93(6), 1203–1213. https://doi.org/10.1111/j.1365-2745.2005.01039.x
- Wolch, J. R., Byrne, J., & Newell, J. P. (2014). Urban green space, public health, and environmental justice: The challenge of making cities 'just green enough.' *Landscape and Urban Planning*, 125, 234–244. https://doi.org/10.1016/j.landurbplan.2014.01.017
- Woodroffe, R., & Ginsberg, J. R. (1998). Edge Effects and the Extinction of Populations Inside Protected Areas. *Science*, 280(5372), 2126–2128. https://doi.org/10.1126/science.280.5372.2126

Figures



Figure 1. A visual representation of bird communities within protected forests and the biodiversity experiences people may have when visiting them. Richness is represented by the total number of species seen within the protected forest. Some species can be found only within the forest and not within the matrix habitat, as may be the case for species that are dependent on forest habitat or are of conservation concern (depicted in orange; see text for definitions). Community species dissimilarity, or uniqueness, is represented by a lack of overlap in species composition between matrix habitat and the protected forest. In this figure, people that visit these two protected forests (to the right or left) will experience higher species may also be found in the urban habitat too (high richness, low species dissimilarity). In contrast, visitors at a protected forest surrounded by natural matrix habitat will see species they do not regularly encounter (high species dissimilarity), including rare or declining species (highlighted in orange). However, the protected forest may have lower than average species richness.



Figure 2. Four different metrics are used to evaluate the same protected forest bird diversity. Forested protected areas are classified by their size (x-axis) and the their surrounding matrix habitat (circle for agricultural, triangle for developed, square for natural). A) Total species richness within a forest. B) Species compositional similarity between a protected forest and its surrounding matrix habitat. C) Number of forest dependent species within each forest. D) Number of species of conservation concern (CC) within each forest. Highlighted in red across all figures is the same protected forest, illustrating the degree to which a single forest can vary in the biodiversity experiences it provides.

Table 1: Definitions of biodiversity metrics, how they are referred to in the paper,

and how people may respond to these different metrics.

Biodiversity metric	Biological meaning	People's response to metric
Richness	Total number of species in a given protected area.	People show increased health and mental benefits, although they are unable to identify areas of high richness (Nielsen and Hansen 2007, Pett et al. 2016).
Rarity	Species that are uncommon or occur at low numbers and only in specific patches. Often species of conservation concern.	People often look for specific species in natural areas and gain benefits only from the presence of these species. Uncommon species can be especially valued (Rehdanz 2007; Chourchamp et al. 2006; Holden and McDonald-Madden 2017)
Uniqueness	Species compositions that are distinctly different from surrounding locations. Protected areas contain species that can only be experienced there.	People respond to novelty, relative to what they encounter otherwise. Sites that provide a different set of species than the surrounding landscape are associated with larger health benefits (Shanahan et al. 2015; 2016).

Table 2: The richness, number of forest dependent species, and number of species of conservation concern (CC) within each protected forest, divided into three groups by surrounding matrix habitat type. Standard deviation shown in parenthesis. Letters denote statistically significant differences between matrix habitat groups.

Matrix Type	Total Richness	Forest Specialists	Species of CC
Agricultural	18.7 (5.15) ^A	7.58 (2.39) ^{C, D}	4.53 (2.25) ^E
Developed	14.8 (3.00) ^B	6.76 (2.14) ^D	3.48 (1.33) ^E
Natural	16.3 (4.03) ^{A,B}	8.69 (2.27) ^c	4.25 (0.93) ^E

Table 3: Difference in protected forest biodiversity as compared to its surrounding matrix habitat. Degree of compositional dissimilarity between a protected forest bird community and its surrounding matrix habitat is shown in parenthesis.

Matrix Type	⊿Richness	∆Forest	Δ Species of	Dissimilarity
		Specialists	СС	
Agricultural	-2.16	4.11***	-3.84***	0.686 (0.27) ^A
Developed	-2.33**	3.53***	1.28	0.576 (0.31) ^{A,B}
Natural	1.03	1.24	0.95	0.397 (0.15) ^в
*** p <0.0001 *	*p < 0.001	*p < 0.05		

Table 4: Relationship between size of protected forests and its richness, number of species of conservation concern, number of species that are forest dependent, and its compositional dissimilarity as compared to its surrounding matrix habitat. All results are outputs from linear models and are reported in units per ha.

Matrix Type	Richness	Forest	Species of CC	Dissimilarity		
	x Size	Specialists	x Size	x Size		
		x Size				
Agricultural	0.003	0.045*	0.004	6.1 x 10 ⁻ ³ **		
Developed	-0.035*	0.033*	-0.005	4.1 x 10 ⁻ ³ *		
Natural	-0.007	0.012	-0.010	5.6 x 10 ⁻ ₄		
*** p <0.0001 **p < 0.001 *p < 0.05						

Supplements

 ${\bf Figure \ S1. \ NMDS \ results \ used \ to \ calculate \ community \ dissimilarity}$

Figure S2. Species accumulation curves for the forests sampled separated by matrix type



Supplemental Figure 1. We produced an NMDS to assess species dissimilarity between the bird community within a protected forest and the surrounding matrix habitat. Using the NMDS output, we matched each protected forest to its matrix habitat (left). For example, we highlight one protected forest in green and its corresponding matrix habitat in red. In the right figure, we measure the Euclidean distance between these two points to determine how dissimilar in species composition the two location are to one another. The closer the points, the more similar, and vice versa.



Supplemental Figure 2. Species accumulation curves for each of the protected forests sample, divided into three groups based on their surrounding matrix habitat type (yellow = agricultural, urban = gray, and natural = green). Each forest was sampled over 15 days within a 60-day window when all birds were breeding within 2016.

Things that go bump in the light: artificial light increases abundance of arthropod predators, detritivores, and parasites

Abstract

From harnessing fire to inventing the lightbulb, humans have a long history of lighting up the night. Despite this history, the widespread impacts of light pollution on ecological systems have largely been ignored. The few studies that have investigated community-level responses to artificial light typically do so by comparing lit to unlit areas, and fail to address how naïve communities respond to the initial introduction of artificial light. We address this shortcoming by documenting how a forest arthropod community previously unaffected by ecological light responds to the introduction and subsequent removal of nighttime artificial light. Using an array of landscaping lights placed above pitfall traps, we track community composition over fifteen consecutive nights including a five-night prelight period, five-night during-light period, and five-night post-light period. Our results highlight a trophic level response to artificial nighttime lighting where arthropod detritivores, predators, scavengers, and parasites all increased in abundance, but herbivores decreased. Furthermore, we show that associated trophic shifts occurred immediately upon the introduction of artificial light, but trophic levels almost completely reverted to their pre-light state once light was removed. We suggest that trophic shifts may be common as light pollution increases globally, implicating artificial light as a cause of global decreases in arthropod abundance.

Keywords: light pollution, artificial light at night, community shifts, arthropods, mechanistic urban ecology

Introduction:

The Anthropocene is defined by high levels of human influence resulting in atmospheric, geologic, hydrologic, and biospheric shifts (Waters et al. 2016). These shifts are often linked to increasing human population and have been highlighted by researchers and members of the media over the last three decades (Vitousek et al. 1997, Boykoff and Boykoff 2007). Many changes caused by humans are easily observed (e.g. increased plastic pollution) or are widely discussed in and out of scientific circles (e.g. increased climate variability), however, subtler changes often go unnoticed. One such impact, and an emerging research topic, is ecological light pollution. Increases in population and urbanization along with the invention and adoption of new technologies such as light-emitting-diodes (LEDs) have disturbed light-dark cycles on a global scale (Longcore and Rich 2004, Pawson and Bader 2014). Currently, artificial light is a common part of most nightscapes with many areas, especially cities, regularly brighter than nights during the full moon (Davies et al. 2013). Artificially bright nights have been identified as a critical and growing threat to biodiversity; each year an additional 6% of total land is influenced by nighttime light pollution (Smith 2008, Hölker et al. 2010, Bennie et al. 2015). With most of the world impacted by artificial light at night (ALAN) and more areas affected each year, understanding how artificial light changes and shapes ecological communities is critical to future conservation, management, and city planning practices.

Many studies investigate how natural light levels impact species' reproduction, migration, foraging, predation, signaling, and other behavioral patterns (Baker and Cardé 1979, Brown et al. 1988, Warrant and Dacke 2011,

Packer et al. 2011). However, these patterns have been suggested but rarely experimentally studied in relation to artificial lighting. To date, artificial light research has used urban-rural gradients to compare community composition and species' abundance in areas of high ALAN to areas without ALAN (Rich and Longcore 2006). Other studies have compared individual behaviors seen around artificial lights to behaviors seen in non-light disturbed environments (Polak et al. 2011, Davies et al. 2012, Becker et al. 2013, Gaston et al. 2013, but see for a manipulative experiment Meyer and Sullivan 2013). One of the most striking conclusions from these studies is that predatory species are disproportionally attracted to artificial light compared to other trophic levels. The resulting increase in predator abundance around lights has become known as the *night-light niche* (Hill 1990, Schwartz and Henderson 1992, Heiling 1999). In cases in which urbanrural gradients are used to look for evidence of night-light niche, increased predation may instead be responding to underlying changes in urban environments or supplemental food sources that are unrelated to increased artificial light (Warren et al. 2006, Shochat et al. 2006). Additionally, because these studies compare communities impacted and unaffected by ALAN, they lack comparisons to pre-light communities and thus fail to address potential trophic differences stemming from urban-rural landscape dissimilarities (Clergeau et al. 1998, Williams et al. 2005, Knapp et al. 2008).

Using an array of pitfall traps and artificial lights, we seek to document the *night-light niche* by experimentally investigating how naïve forest arthropod communities (i.e. a community that has not previous experienced light pollution) respond to the introduction of ALAN. Through experimental manipulation, we

established ALAN as a mechanistic driver in community change by monitoring compositional change before and after the introduction of artificial light. We continued to sample after the removal of ALAN to investigate if these communities returned to their pre-disturbed state, or if artificial light impacts communities even when it is turned off or has been permanently removed (see Davies et al. 2012). Our results provide insight into how arthropod communities will respond as light pollution spreads to non-light-polluted environments.

Methods

Study Site

We conducted our study at Rutgers University's Hutcheson Memorial Forest Center (HMFC), an ecological preserve and research facility located in Franklin Township, New Jersey. HMFC, which consists of nearly 200 ha of protected old growth oak-hickory forest, provides an ideal area to study light pollution because it is undeveloped and closed to the public. These two factors significantly mitigate the amount of ecological light pollution in the area, and prevent human disturbances from influencing our data. The study was conducted along a pathway, 10 m wide, that was created during the installation of a deer exclosure fence during the summer of 2015. Following the fence construction, plants naturally recolonized the path so that at the time of study it was dominated by a patchwork of grasses and herbs. The pathway was semi-regularly mowed 5-6 times per summer to a height of approximately 2 in including three days prior to the start of our experiment.

Experimental Design

We conducted a pitfall trap experiment for fifteen days in August of 2016. Pitfall traps were comprised of two plastic party cups, one inside the other, buried flush with the ground. This configuration resulted in a 12 cm deep pitfall trap with a 9.5 cm diameter opening. The double cup design allowed us to easily remove and replace traps without disturbing the soil. Approximately 1/8th of the pitfall trap was filled with water and unscented soap to trap any arthropod that fell into the trap. A total of 20 traps were set with each trap placed between 15 and 20 m apart. An LED landscaping light was suspended 2.5 m above 10 of the traps (experimental traps), while the other 10 traps without suspended lights acted as controls. The lights produced a maximum lux of 1,800 lumens, had a color temperature of 3,000 kelvins, and a wavelength of approximately 550 nanometers. The control traps were interspersed evenly between the experimental traps (see supplement 1).

During each day of the experiment, we sampled twice a day 20 minutes before civil dawn and 20 minutes after civil dusk. We selected civil dawn and dusk (when the sun is 6 degrees below the horizon) to sample as this when streetlights and house lights are typically turned on. Collecting samples twice a day allowed us to distinguish between diurnal and nocturnal communities.

For the first 5 days of the experiment (days 1-5), lights remained off while sampling occurred. For the next 5 days (days 6-10), light was turned on at night after samples were collected at dusk and turned off before samples were collected at dawn (figure 1). For the final 5 days (days 11-15), the lights remained off and sampling continued as normal. All samples were placed in ethanol and stored in a freezer to ensure they were well preserved until identification and sorting.

Identification and Analysis

We identified all caught individuals to the family level. Commonly occurring taxa were identified to the genus or species level. We also categorized caught individuals into flying or non-flying groups and placed them into a functional guild based off dietary information (see supplement 2). As pitfall traps are not ideal for capturing flying arthropods, we did not include these species in our analysis. The removal of flying arthropods also ensures that traps were far enough apart to be considered independent for the sake of analysis. Additionally, all Collembola were removed from our analysis as they were often not identifiable beyond order. The number of Collembola was also an order of magnitude larger than all other taxonomic groups combined.

With the remaining individuals, we compared the average abundance for each night (dusk to dawn) over the three conditions (pre-light, during-light, postlight) for all experimental pitfall traps and all control traps. Comparisons were made using ANOVA in program R version 3.5.1 (R Core Team 2018). We conducted the remaining analysis only on samples collected from experimental pitfall traps. Using the same methods, we compared the average abundance of each guild per night during the three conditions.

Following this analysis, we compared the community composition of individuals we collected each night. Communities were represented by the abundance of each family collected and compared using a principle component analysis (PCA) with package Vegan (Oksanen 2019). We assigned all communities to a cluster based off when the community was collected (i.e. pre-light exposure, during-light exposure, post-light exposure). We compared whether clusters were distinct using permutational multivariate analysis of variance with PERMANOVA and tested for differences in dispersion using betadisper, which are both in package Vegan (Oksanen 2018). Finally, we tested the fit of each community in its assigned cluster using hierarchical clustering and checked the fit of each cluster with package pvclust (Suzuki and Shimodaira 2006). The final step of analysis involved using the results of this PCA to assess the weighting of each family in terms of how important it was to distinguish a particular community composition. All families with over 0.1 or under -0.1 weight were selected to investigate how their abundance changed across the three time periods. The average abundance of these families was compared using ANOVA in R (R Core Team 2018).

Results

Over the course of this experiment, we captured 2,894 individual arthropods representing 11 Classes, 39 Orders, and 136 Families. Average abundance per night did not differ between experimental traps and controls traps during the pre-light and post-light sampling periods. Abundance in the control traps during the light period did not differ from the pre-light and post-light traps, either control or experimental. However, abundance in the experimental traps during the light period was almost twice as high as during the other time periods (Figure 2. ANOVA. p<0.001).

The five most abundant trophic guilds underwent significant shifts in abundance when light was on (figure 3). Increases in the average nightly abundance of detritovores, parasites, predators, and scavengers were evident when compared to pre-light and post-light conditions (ANOVA, p<0.05, p<0.05, p<0.001, p<0.001 respectively). A decrease in guild abundance was seen in herbivore abundance between pre-light conditions and both the during-light and post-light periods (ANOVA. p<0.01, p<0.05). However, herbivore abundance was significantly higher in the post-light period compared to the during-light period (ANOVA. p<0.05).

Our principal component analysis captured 79% of the total variance in community composition using the first two components (Figure 4). We show a significant difference between pre-light and during-light community compositions, as well as during-light and post-light communities (PERMANOVA p<0.001, p < 0.001). This shift in composition was seen immediately, as the assemblage of arthropod species collected on the first night post-light exposure was more similar in composition to all other light-influenced communities than it was to the pre-light community (pvclust. Bootstrap Probability 100). Additionally, the during-light community composition had large dispersion, indicating higher compositional variability between nights and trap locations as compared to both the pre-light and post-light communities (betadisper. p<0.001, p<0.001). We observed no significant difference between the pre-light and post-light communities in composition or dispersion. Nine families were identified as contributing to the differences between the pre/post-light and during light communities. In order of contribution, these families were Carabidae (ground beetles), Gryllidae (crickets), Formicidae (ants), Lycosidae (wolf spiders), Tingidae (lace bugs), Ixodidae (scale ticks), Phalangiidae (harvestmen), Agelenidae (grass spiders), and Armadilididae (sow bugs).

We found that all nine families changed in composition when light was on as compared to when it was off. Agelenidae, Carabidae, Formicidae, Gryllidae, Ixodidae, and Lycosidae all increased in abundance when the light was on, but returned to pre-light levels once the light was off. Armadilididae, Phalagiidae, and Tingidae all showed a reduction in abundance when the light was turned on followed by a return to pre-light levels once lights were removed.

Discussion

Here we contribute to the growing evidence that artificial light influences both the functional and taxonomic structure of communities. Specifically, we provide experimental evidence that the introduction of artificial light increases, or locally clusters, arthropod species. However, this increase in biomass was not uniform among taxa and trophic guilds. We illustrate that not all arthropods show the same affinity towards artificial light, and some taxa and trophic guilds seem to avoid light or decrease in abundance in the presence of light. While detritivores, parasites, predators and scavengers show up to a four-fold increases in abundance, herbivore abundance decreased when light is present. These shifts in predator and scavenger abundance match previously observed results (see Davies et al 2012), but the increases in detritivores and parasites are novel to this study. Our results run counter to observations seen with changing natural lights levels where increased natural light decreases predator activity (Sábato et al. 2006, Packer et al. 2011), thus re-affirming that the *night-light niche* is a novel behavior in response to artificial light.

If artificial lights increase predation pressure around them, they may act as an ecological sink for many arthropod species. Many nocturnal species avoid high levels of light as they are associated with higher predation risks (e.g. Kolter et al. 1992), but the decrease observed in our study is likely due to an increase in predation instead of light avoidance. While all other trophic guilds return to prelight abundances after the light is removed, the herbivores increase in abundance but not to pre-light levels. This evidence suggests that the local herbivore community was reduced in abundance by predators when the lights were on, and only slowly recovered after the removal of light. These results highlight the risk that artificial light sources will act as ecological traps (Szaz et al. 2015), which is especially relevant in a time when global arthropod conservation is of increasing concern.

Currently cities host rich assemblages of native and non-native species and are of growing importance to biodiversity conservation goals (Aronson et al. 2014, Lepczyk et al. 2017). However, it is not always clear what species from the regional pool will be able to adapt and survive in urban environments (Kark 2006; Sorte et al. 2018). As the growth of many current and future cities pose threats to biodiversity hotspots, many researchers have called for a greater understanding of the mechanisms that act as filters and shape urban biodiversity (Cincotta et al. 2000; Shochat et al. 2006). Our results provide mechanistic evidence of light pollution acting as an ecological filter to reduce herbivore populations and speak to a larger pattern of arthropod decline seen worldwide (Raupp et al. 2010; Grubisic et al. 2018). Currently, conservationists look to greenspaces embedded in cities as potential solutions to maintaining urban biodiversity. While urban greenspaces can provide habitat for many species, city planners often increase lighting in parks to increase human safety and usability (McCormack et al. 2010). This creates a conflict that threatens biodiversity as artificial lighting often acts as an ecological trap for arthropods, thus negating the ecological value of protected open spaces (Szaz et al. 2015).

The high levels of mortality associated with artificial light could act as a strong selective pressure for species to avoid artificial lighting. With most cities in a near constant state of brightness, species that live in urban and peri-urban areas already show forms of light avoiding behavior, but no such adaptation has been seen for rural species (Altermatt and Ebert 2016; Hopkins et al. 2018). It is unlikely that species in environments that are currently unaffected by ALAN will be able to adapt at a rate that matches the rapid spread of ALAN to novel environments (Hölker et al. 2010). As a result, the rapid introduction of ALAN, especially in biodiversity hotspots, poses a great threat to species as even a small of amount of light has been shown to cause ecological shifts (Sanders et al. 2018). As cities and ALAN expands, species that are unable to avoid potential ecological traps or increased rates of predation are likely to be lost from the community, suggesting that further investigation into the influence of artificial light biodiversity is needed. Research like ours can contribute to more complex community filter models that will provide a comprehensive understanding of urban/anthropogenic impacts on ecosystem function and biodiversity. Just as we consider novel strategies to combat impacts of climate change (e.g. assisted migration plans) and increased pollution (e.g. the bioengineering of plastic consuming microbes), so must we consider inventive solutions to mitigate the impacts of light pollution. Understanding the influence of artificial light on communities and the resulting ecological interactions that may occur is a critical first step in identifying appropriate actions to take for the future planning and policy associated with artificial light.

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References

- Altermatt, F., and D. Ebert. 2016. Reduced flight-to-light behaviour of moth populations exposed to long-term urban light pollution. Biology Letters 12:20160111.
- Baker, T. C., and R. T. Cardé. 1979. Endogenous and exogenous factors affecting periodicities of female calling and male sex pheromone response in Grapholitha molesta (Busck). Journal of Insect Physiology 25:943–950.
- Becker, A., A. K. Whitfield, P. D. Cowley, J. Järnegren, and T. F. Næsje. 2013. Potential effects of artificial light associated with anthropogenic infrastructure on the abundance and foraging behaviour of estuary-associated fishes. Journal of Applied Ecology 50:43–50.
- Bennie, J., J. P. Duffy, T. W. Davies, M. E. Correa-Cano, and K. J. Gaston. 2015. Global Trends in Exposure to Light Pollution in Natural Terrestrial Ecosystems. Remote Sensing 7:2715–2730.
- Boykoff, M. T., and J. M. Boykoff. 2007. Climate change and journalistic norms: A casestudy of US mass-media coverage. Geoforum 38:1190–1204.
- Boyle, K. J., S. D. Reiling, and M. L. Phillips. 1990. Species substitution and question sequencing in contingent valuation surveys evaluating the hunting of several types of wildlife. Leisure Sciences 12:103–118.
- Brown, J. S., B. P. Kotler, R. J. Smith, and W. O. Wirtz. 1988. The effects of owl predation on the foraging behavior of heteromyid rodents. Oecologia 76:408–415.
- Clergeau, P., J.-P. L. Savard, G. Mennechez, and G. Falardeau. 1998. Bird Abundance and Diversity along an Urban-Rural Gradient: A Comparative Study between Two Cities on Different Continents. The Condor 100:413–425.
- Davies, T. W., J. Bennie, and K. J. Gaston. 2012. Street lighting changes the composition of invertebrate communities. Biology Letters:rsbl20120216.
- Davies, T. W., J. Bennie, R. Inger, and K. J. Gaston. 2013. Artificial light alters natural regimes of night-time sky brightness. Scientific Reports 3:1722.
- Gaston, K. J., J. Bennie, T. W. Davies, and J. Hopkins. 2013. The ecological impacts of nighttime light pollution: a mechanistic appraisal. Biological Reviews 88:912– 927.
- Grubisic, M., R. H. A. van Grunsven, C. C. M. Kyba, A. Manfrin, and F. Hölker. 2018. Insect declines and agroecosystems: does light pollution matter? Annals of Applied Biology 173:180–189.
- Heiling, A. M. 1999. Why do nocturnal orb-web spiders (Araneidae) search for light? Behavioral Ecology and Sociobiology 46:43–49.
- Hill, D. 1990. The impact of noise and artificial light on waterfowl behavior: a review and synthesis of the available literature.
- Hölker, F., C. Wolter, E. K. Perkin, and K. Tockner. 2010. Light pollution as a biodiversity threat. Trends in Ecology & Evolution 25:681–682.
- Hopkins, G. R., K. J. Gaston, M. E. Visser, M. A. Elgar, and T. M. Jones. 2018a. Artificial light at night as a driver of evolution across urban–rural landscapes. Frontiers in Ecology and the Environment 16:472–479.
- Hopkins, G. R., K. J. Gaston, M. E. Visser, M. A. Elgar, and T. M. Jones. 2018b. Artificial light at night as a driver of evolution across urban-rural landscapes. Frontiers in Ecology and the Environment 16:472–479.

Knapp, S., I. Kühn, V. Mosbrugger, and S. Klotz. 2008. Do protected areas in urban and rural landscapes differ in species diversity? Biodiversity and Conservation 17:1595–1612.

Kolter, B.P., Blaustein, L., and Brown, J.S. 1992. Predator facilitation: the combined effects of

snakes and owls on the foraging behavior of gerbils. Annales Zoologici Fennici 29(4) 199-206

- Longcore, T., and C. Rich. 2004. Ecological Light Pollution. Frontiers in Ecology and the Environment 2:191–198.
- McCormack, G. R., M. Rock, A. M. Toohey, and D. Hignell. 2010. Characteristics of urban parks associated with park use and physical activity: A review of qualitative research. Health & Place 16:712–726.
- Meyer, L. A., and S. M. P. Sullivan. 2013. Bright lights, big city: influences of ecological light pollution on reciprocal stream–riparian invertebrate fluxes. Ecological Applications 23:1322–1330.
- Packer, C., A. Swanson, D. Ikanda, and H. Kushnir. 2011. Fear of Darkness, the Full Moon and the Nocturnal Ecology of African Lions. PLOS ONE 6:e22285.
- Pawson, S. M., and M. K.-F. Bader. 2014. LED lighting increases the ecological impact of light pollution irrespective of color temperature. Ecological Applications 24:1561–1568.
- Polak, T., C. Korine, S. Yair, and M. W. Holderied. 2011. Differential effects of artificial lighting on flight and foraging behaviour of two sympatric bat species in a desert. Journal of Zoology 285:21–27.
- Sábato, M. A. L., L. F. B. de Melo, E. M. V. Magni, R. J. Young, and C. M. Coelho. 2006. A note on the effect of the full moon on the activity of wild maned wolves, Chrysocyon brachyurus. Behavioural Processes 73:228–230.
- Schwartz, A., and R. Henderson. 1992. Amphibians and Reptiles of the West Indies: Descriptions, Distributions, and Natural History. The Quarterly Review of Biology 67:380–381.
- Shochat, E., P. S. Warren, S. H. Faeth, N. E. McIntyre, and D. Hope. 2006. From patterns to emerging processes in mechanistic urban ecology. Trends in Ecology & Evolution 21:186–191.
- Smith, M. 2008. Time to turn off the lights. Nature 457:27.
- Suzuki, R., and H. Shimodaira. 2006. Pvclust: an R package for assessing the uncertainty in hierarchical clustering. Bioinformatics 22:1540–1542.
- Szaz, D., G. Horvath, A. Barta, B. A. Robertson, A. Farkas, A. Egri, N. Tarjanyi, G. Racz, and G. Kriska. 2015. Lamp-Lit Bridges as Dual Light-Traps for the Night-Swarming Mayfly, Ephoron virgo: Interaction of Polarized and Unpolarized Light Pollution. PLOS ONE 10:e0121194.
- Vitousek, P. M., H. A. Mooney, J. Lubchenco, and J. M. Melillo. 1997. Human Domination of Earth's Ecosystems. Science 277:494–499.
- Warrant, E., and M. Dacke. 2011. Vision and Visual Navigation in Nocturnal Insects. Annual Review of Entomology 56:239–254.
- Warren, P., C. Tripler, D. Bolger, S. Faeth, N. Huntly, C. Lepczyk, J. Meyer, T. Parker, E. Shochat, and J. Walker. 2006. Urban Food Webs: Predators, Prey, and the

People Who Feed Them. The Bulletin of the Ecological Society of America 87:387–393.

- Waters, C. N., J. Zalasiewicz, C. Summerhayes, A. D. Barnosky, C. Poirier, A. Gałuszka,
 A. Cearreta, M. Edgeworth, E. C. Ellis, M. Ellis, C. Jeandel, R. Leinfelder, J. R.
 McNeill, D. deB Richter, W. Steffen, J. Syvitski, D. Vidas, M. Wagreich, M.
 Williams, A. Zhisheng, J. Grinevald, E. Odada, N. Oreskes, and A. P. Wolfe.
 2016. The Anthropocene is functionally and stratigraphically distinct from the
 Holocene. Science 351:aad2622.
- Williams, N. S. G., J. W. Morgan, M. J. Mcdonnell, and M. A. Mccarthy. 2005. Plant traits and local extinctions in natural grasslands along an urban–rural gradient. Journal of Ecology 93:1203–1213.

Figures:



Figure 1: A photo of the experimental design showing two of the light installations. Photo taken fifteen minutes prior to dawn. Photo by Jeff Brown.



Figure 2: Average abundance caught across all traps per night during the three time periods. During all three time periods, control showed no significant change in abudnace and was also not significantly different than the pre light or post light treatment groups. The only difference in the number of arthropods captured was seen during the treatment group when lights were on.



Figure 3: Average abundance caught across experimental traps per night during the three time periods separated by functional guild. Significant differences are seen in all guilds when the light is on compared to before the light was turned on and after the light was turned off. Only hebrivores show a significant difference between the pre and post light conditions.



Figure 4: Results of a principal component analysis with the communities from each night of the experiment. Each dot represents one night during the experiment. Clusters are set around each time period and no significant difference is seen between the pre and post light clusters but the during light custer is significantly different than the other groups. Families with the weighting under -.1 or over .1 on either PC1 or PC2 are displayed with arrows and visual representation. Two families, Agelenidae and Armadilididae have been omitted for clarity.


Figure 5: Shifts in key families identified by the weighting of the PCA. Significant increases in abundance are seen when light is on for Agelenidae, Carabidae, Formicidae, Gryliidae, and Lycosidae. Armadilididae Phalagiidae, and Tingidae are decrease in abundance in the presence of light.

Supplemental Materials

- ${\bf S1.}$ Additional information on lighting used for study design.
- **S2.** Results for light levels throughout the experiment.

S1.

LED landscaping lights were used as the source of light pollution for this experiment. These lights were selected because they are commonly used in residential areas, are associated with urbanization, and have similar wavelengths to the streetlights common in most developed areas (Nights in Davis, and Street lights in Urban Areas). Lights were suspended from a height of two meters and light level was measured from the opening of the pitfall traps. Light levels were measured each night before collection both over traps with and with lights. Ambient light levels were also measured every ten minutes before and after collection and ambient light levels were also measured over the course of twenty-four hours for three days. The of the photometer used ranged from 0.01-400,000 lux **S2.** All traps spent most of the diurnal periods experience light levels of ~100,000 lux (i.e. full daylight) although traps did experience light levels that dipped to 2,000-10,000 lux as cloud cover shifted during the day. Light levels at night (i.e. after civilian dusk) ranged from 700 lux to 0.00 lux for control traps and during the pre and post light time periods. Light levels steadily decreased from civilian dusk until an hour after dusk in which they steadied at levels less than 1 lux (average 0.06 lux, standard deviation 0.01 lux). Light level at night over traps during the time period light was on was significantly higher (p<0.001) than ambient light levels with an average light level of 10.31 lux (standard deviation 1.12 lux)