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A Hollywood drama of butterfly extirpation and persistence over a century of urbanization

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Abstract Few long-term examples exist of wildlife population trends in urban environments despite the recent recognition of the importance of biodiversity in cities. Founded in 1896, Griffith Park's over 1,700 ha in Los Angeles adjacent to Hollywood represent the largest municipal park in California. Through the 1920s, biologists studied the natural area with great interest but in the decades that followed, little fieldwork was conducted here as Los Angeles developed into a megacity surrounding the park. We combined thorough examination of Griffith Park historical field notes and specimen records (1900–1960) with recent field surveys (2011–2012) to determine (1) the extent of urbanization impacts on butterfly extirpation and persistence and (2) how butterfly traits and host plant relationships might be contributing to butterfly species status. Here we document multiple local butterfly extinctions in Griffith Park; 10 species or 18 % of the historically reconstructed community. Many of these species were lost early in the twentieth century, highlighting the importance of the historical record in understanding urban biodiversity patterns and trends. An analysis of larval host plant status and relationships suggests that a primary factor determining butterfly presence or extirpation is the abundance of the larval host plant in the park, in addition to host plant specificity. Despite these extirpations, we also found that the majority (over 80 %) of native butterfly species have persisted including species of conservation interest. While urban parks certainly suffer from surrounding anthropogenic pressure and impacts, this study also demonstrates the potentially high and underappreciated conservation and ecological value of urban parks.

Keywords Biodiversity · Introduced species · Habitat degradation · History · Lepidoptera

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Introduction

Urbanization can result in multiple land use and climatic changes on ecosystems at local, regional and global scales (Grimm et al. 2008). Direct habitat loss, habitat fragmentation, invasive species and pollution through urbanization have all been shown to impact biodiversity in often complex ways (Weiss 1999; McKinney 2002; Magle and Crooks 2009; Dures and Cumming 2010; Shochat et al. 2010; Kowarik 2011). Understanding urbanization's influence on ecological communities has therefore recently emerged as a central issue in biodiversity conservation (Dearborn and Kark 2010; Kattwinkel et al. 2011).

Despite the increased interest in urban ecological systems few studies have explored population trends over long time periods (e.g., decades) in natural communities within urban environments (Marzluff et al. 2001; Gaston 2010; Shultz et al. 2012). Long-term conservation studies in general are uncommon (Bonebrake et al. 2010) despite the importance of historical context and temporal dynamics in urban and environmental research (Swetnam et al. 1999; Ramalho and Hobbs 2012). Thus, the long-term effect of urbanization on many ecosystems and their dependent species remains largely unknown and unquantified.

Urban arthropods are especially understudied despite being crucial components and indicators of urban ecosystems and biodiversity (McIntyre 2000; Magle et al. 2012). For Lepidoptera, surveys across spatial gradients indicate that urbanization generally causes negative impacts on diversity (Blair 1999; Hardy and Dennis 1999; Clark et al. 2007; Konvicka and Kadlec 2011), though butterfly species numbers can remain relatively high in some highly urbanized landscapes (Koh and Sodhi 2004; Giuliano et al. 2004; Jones and Leather 2012). Studies have shown that both local scale variables (e.g., floral diversity, vegetation cover) and landscape level variables (e.g., patch isolation, matrix configuration) can determine butterfly diversity in urbanized areas (Brown and Freitas 2002; Öckinger et al. 2009; Matteson and Langellotto 2010; Williams 2011; Lizée et al. 2012; Ramírez Restrepo and Halffter 2013; Shwartz et al. 2013).

However, long-term trends in urban insect diversity are rarely known or studied (Fattorini 2011a). Several Australian butterfly extirpations have been documented during twentieth century urbanization (New and Sands 2002). In the San Francisco Bay Area, iconic species such as the Xerces blue (*Glaucopsyche xerces*) are also known to have gone extinct due to development in the region (Connor et al. 2002). In one exceptionally detailed study, Fattorini (2011b) showed that most butterfly extinctions documented in urban Rome took place from 1900 to 1949 such that the majority of butterflies currently in Rome are tolerant to urban conditions (those that were not were extirpated long ago). The lack of historical and temporal data for insects in urban areas therefore hampers our ability to effectively conserve them or understand how urbanization fully impacts biodiversity, since current communities may bear little resemblance to those present historically (Fattorini 2011b).

In this study we took advantage of a particularly robust historical dataset on butterflies from the early 1900s in Griffith Park, Los Angeles to examine the extent of butterfly extirpation and persistence that has occurred in response to the intensive twentieth century urbanization that transformed coastal southern California from an agricultural area with scattered towns to the mega-city of today. Even the park's interior was impacted by twentieth century urbanization; in 1904, *Science* (Vol. 20, p. 616) reported on plans in Griffith Park for timber production within the "waste piece of land" that resulted in large areas of native scrub being afforested with non-native conifers and eucalyptus. Several fires, including large burns over hundreds of hectares in 1923 and 2007, also affected portions of the park, and ongoing non-native species invasions, particularly those of non-native grasses, continue to take their toll on native flora and fauna, aided by annual "fuel modification" (vegetation clearing) along fire roads and trails throughout much of the park. Taken together, the process of urbanization and disturbance in and around Griffith Park has led to multiple large scale changes including direct habitat loss (e.g., paving and development), exotic species invasions, and disturbance (Cooper and Mathewson 2009).

We combined historical data collection (museum records, literature etc.) with contemporary, systematic butterfly surveys in Griffith Park to compare the modern and historical butterfly communities. We then analyzed the traits of persisting and extirpated butterflies to uncover possible factors that would favor extirpation or persistence in response to urbanization. Specifically we tested whether several variables, including wingspan, host plant specificity, non-native host plant use or host plant abundance had any relationship to the current status of butterflies in Griffith Park. Thus, we (1) document urbanization consequences reflected by long-term trends in butterfly extirpation and persistence and (2) examine possible factors contributing to butterfly species status under urbanization pressures.

Materials and methods

Study site: Griffith Park

Centrally located within Los Angeles, California USA (Fig. 1), Griffith Park is a 1,700-ha landscape of natural wildland surrounded by park-like/lawn habitat at the far eastern end of the Santa Monica Mountains, within an area that experienced rapid development and associated changes over the past century as the metropolis grew around it (Fig. 2; Eberts 1996). The natural component of the Griffith Park landscape consists of mixed chaparral, scrubland and oak woodland habitats on steep, rugged slopes (Cooper and Mathewson 2009). Development in and around the park has been extensive over the past century (see the Introduction as well as Cooper and Mathewson 2009 for details).

From the 1910s through the 1930s, Griffith Park was especially popular among naturalists in the region, including early California botanists and zoologists; the narrowly-endemic butterfly *Lycaena arota nubila* (Lycaenidae), the cloudy tailed-copper, was described from collections in the park in 1922 by John Adams Comstock (1926), a local lepidopterist who kept meticulous notes on walks in the park, and who later went on to write the early field guide *The Butterflies of California* (1927). Today, over 12 million people visit the park every year (Trust for Public Land 2010) for hiking and famous attractions such

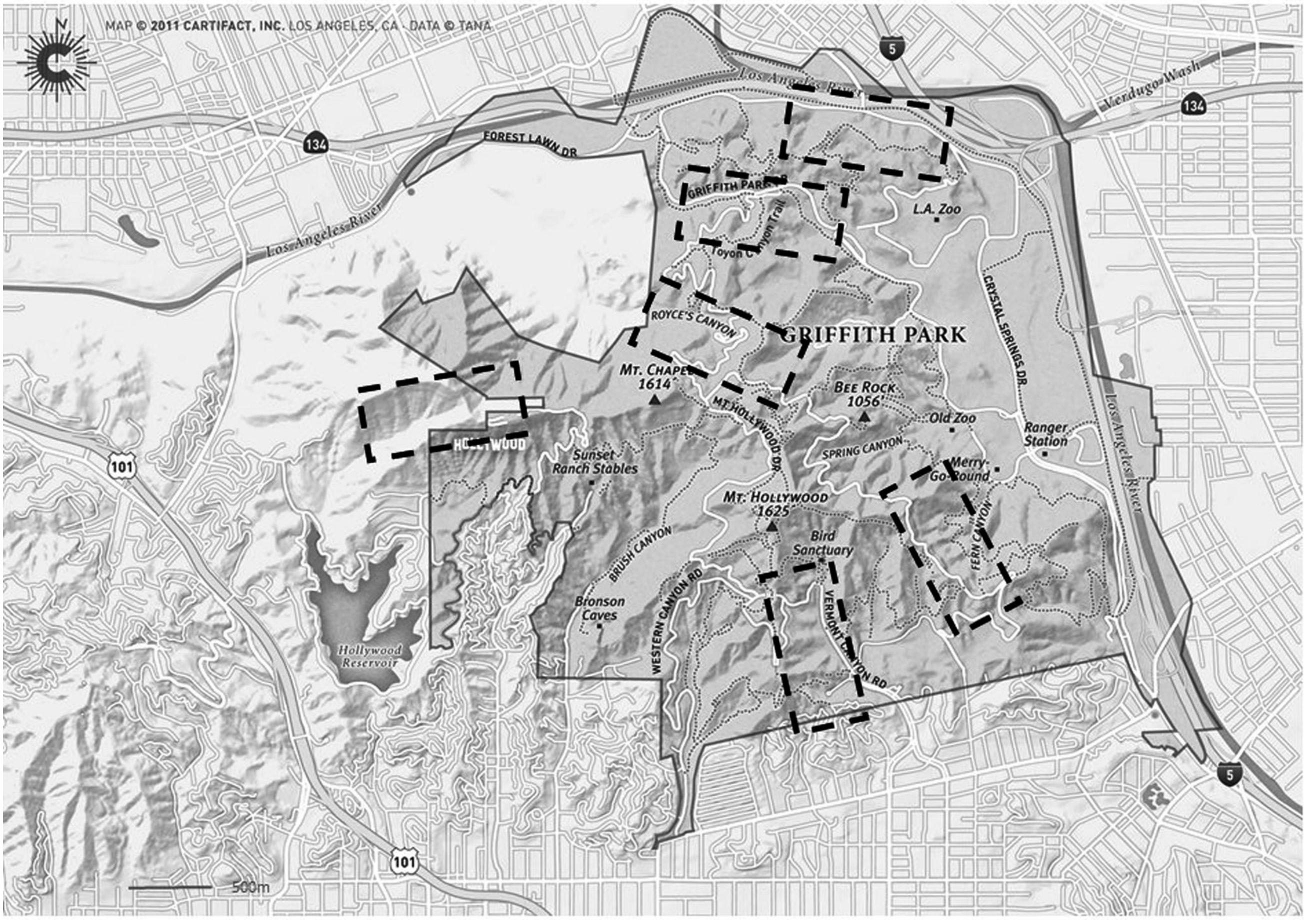

Fig. 1 Griffith Park is surrounded by urbanization with Burbank to the north, Glendale to the east, Hollywood and downtown Los Angeles to the south and the Hollywood Hills to the west. The six primary sampling sites are indicated by *dashed boxes*; Skyline Trail, Oak Canyon, Royce's Canyon, Wonder View Trail, Mineral Wells Trail and Vermont Canyon (from *top* to *bottom*)

as the L.A. Zoo, which has an inevitable impact on local vegetation through trampling, dog waste, and other factors (Cooper and Mathewson 2009).

Historical records (1900–1960) and modern surveys (2011–2012)

We examined museum specimens, field notes and published records for data on historical presence of all butterflies in Griffith Park. Early butterfly records were largely derived from specimens collected in Griffith Park between 1920 and 1960 (with a few records pre-1920) by Comstock and others that were subsequently deposited at the Natural History Museum Los Angeles (NHMLA). We also examined field notes from Comstock dating back to 1917 and relied on other published data (mostly from Gunder 1930) for both locality data and observations. We restricted our scope specifically to records from Griffith Park but also reviewed nearby locality records (e.g., "Hollywood Hills", "Burbank") for species lacking a specific Griffith Park record but likely to have been present there at the time based on habitat type which was assessed from both historical photos, maps and plant collections (Cooper 2011).

We (TCB) monitored butterflies in Griffith Park in 2011 and 2012 by surveying over 71 days across six sites around the park (Fig. 1). Butterflies were censused using transect walks based on the Pollard method (Pollard and Yates 1993, see also Bonebrake and Sorto 2009) from February 2011 to August 2012. Each transect took approximately an hour to complete. Sites were sampled throughout the year (typically each site sampled every other month) in order to maximize detection probability by capturing the breadth of seasonal variation exhibited by California butterfly communities (Pellet 2008). We spaced six primary sites and transects widely to maximize coverage of the park's varied terrain and habitat (Fig. 1), and only sampled on days ideal for butterfly flight: low cloud cover, minimal winds and high air temperatures (>20 °C). For each sampling event we identified and counted all butterflies crossing within a five meter box around the surveyor (Pollard and Yates

Fig. 2 Western Ave in Hollywood California in 1906 (*top panel* Los Angeles Public Library Photo Collection). The tallest peak in the background is Mt. Hollywood and the peak in the foreground is where the Griffith Observatory would be built two decades later. The same location in 2011 (*bottom panel* Timothy C. Bonebrake)

1993). Most individuals were identified on the wing but some individuals were captured and/or photographed for closer inspection when needed. Nearly all butterflies in the park were easily identified upon close examination; however distinguishing *Erynnis tristis* Edwards (Hesperiidae) and *E. funeralis* Scudder & Burgess (Hesperiidae) can be very difficult in this part of their range (Emmel and Emmel 1973). Therefore during transect counts we only identified to genus for *Erynnis* (although we did confirm the presence of *E. tristis* and *E. funeralis* in Griffith Park we found no other *Erynnis* species). We followed the nomenclature of Pelham (2008).

We developed a master list of all resident butterflies in the Los Angeles area and to Griffith Park specifically, excluding only those butterflies with few ("accidental") or questionable records in the Griffith Park area. Thus, we eliminated from our analysis species such as *Nathalis iole* Boisduval (Pieridae) and *Nymphalis californica* Boisduval (Nymphalidae) even though these species could conceivably have been found in the park. For each species known to occur or to have regularly occurred in Griffith Park we assigned the following categories: "confirmed historical" (multiple historical reports or specimens from Griffith Park), "probably historical" (no records, but the species likely occurred based on nearby historical records in similar habitat), "confirmed modern" (recent photographs/observations), "likely extirpated" (no recent photographs/observations) and finally "unknown modern status" for species for which we have a reasonable expectation that the butterfly might be there despite our sampling effort (particularly if the butterfly is small/inconspicuous or is typically sparsely distributed within its range).

The opportunistic-type sampling that makes up the majority of the historical records does not well match the methodology of the line transect-type contemporary surveys. However, a comparison between the two datasets is warranted for a variety of reasons. First and foremost, despite such an "imperfect match" the use of natural history records in the context of presence/absence data and species declines can be informative and is often our only data source for looking at long-term trends (Shaffer et al. 1998). Secondly, we also undertook opportunistic sampling (a running list of all butterfly species observed while in the park was kept) between 2007 and 2010 (over 100 h) but observed no species additional to those observed during the 2011–2012 transects. This suggests that the contemporary surveys were at least somewhat comparable (and likely more comprehensive) than simple opportunistic sampling. Finally, our classification of species was sensitive to the fact that our two years of transect surveys had some limitations and likely imperfect detection (see above paragraph). Such species were classified as "unknown modern status".

Butterfly traits, host plants and data analysis

Host plant identification for each butterfly species was determined using Emmel and Emmel (1973), Orsak (1977) and Garth and Tilden (1986). Based on previous plant surveys in Griffith Park (Cooper 2011) we estimated whether the host plants are now present or rare (and possibly absent) in the park (Table S1). While contemporary plant observations in Griffith Park have been fairly comprehensive (e.g. Cooper and Mathewson 2009; Cooper 2011), data on the historical Griffith Park plant community, such as population estimates and reliable vegetation mapping, are more limited. Thus, we cannot make inferences as to the trends in plant status: only whether or not a given species is now present or rare. For *Coenonympha tullia* Müller and *Cercyonis sthenele* Boisduval, both grass-feeding species, the host plant species are unknown so these species were left out of the host plant status analysis. Finally, the majority of butterfly host plant relationships, usage and preferences have not been verified within Griffith Park itself, only for the wider area (e.g., California). Accordingly, our data on host plant status are only a first approximation.

We also determined whether or not each of the species has been documented as using non-native host plants using the (moderate to high confidence only) records of Graves and Shapiro (2003). We estimated specificity as the number of known host genera used by the species using data directly from Forister et al. (2011) and supplemented by information provided by Garth and Tilden (1986). In addition to host plant relationships, other traits in butterflies are known to influence persistence ability in changing landscapes, especially body size (Shahabuddin and Ponte 2005). Wingspan can be used as an index for both body size and dispersal capability in butterflies (Sekar 2012). Wingspan data were obtained from Opler et al. (2013).

We used both univariate and multivariate approaches to analyze the pattern between butterfly host plant traits, wingspan and butterfly status following Koh and Sodhi (2004). We did a binomial logistic regression for each of the independent variables (host plant status, non-native host plant usage, host plant specificity and wingspan) and the status of the butterfly (either common or extinct/rare, with rare defined as fewer than three observations of the species over the course of the sampling). We additionally ran each regression using butterfly family as a covariate to partially account for lack of phylogenetic independence (Koh et al. 2004). Our multivariate approach generally followed Soga and Koike (2013a). Using the "dredge" function from the MuMIn package (Bartoń 2012), we generated a suite of multiple logistic regression models using all the variables and selected the models of ΔAICc less than 4 from the model with the lowest AICc score. We then applied a model averaging ("model.avg", Bartoń 2012) to calculate relative variable importance as the sum of the Aikake weights over the best candidate models examined (Burnham and Anderson 2002). All analyses were implemented in R 3.0.2 (R Development Core Team 2010).

Results

During the butterfly surveys we counted 1,294 total individual butterflies of 39 species (Table 1). We are unsure of the current status of five species, including *Limenitis lorquini* Boisduval (Nymphalidae) and *Satyrium sylvinus* Boisduval (Lycaenidae), two riparian obligates that may still persist in parts of the Los Angeles River (portions of which are technically within Griffith Park) not covered by the transects. Of the estimated historical community of 55 resident butterfly species in the early twentieth century, we

Table 1 Status of resident Griffith Park butterflies based on historical records and contemporary surveys

Persisting species (historical and contemporary records)	Extirpated species (confirmed historical records only)	Unknown Status (historical records; current status uncertain)
Papilionidae	Nymphalidae	Pieridae
Papilio zelicaon, P. rutulus, P. eurymedon	*Coenonympha tullia, Cercyonis sthenele, Speyeria callippe comstocki, Euphydryas chalcedona, Chlosyne gabbii, Polygonia satyrus*	*Colias alexandra*
Pieridae	Lycaenidae	Nymphalidae
Pieris rapae, Pontia protodice, Anthocharis sara, Colias eurytheme, Zerene eurydice	*Lycaena helloides, L. xanthoides, Glaucopsyche piasus*	*Danaus gilippus, Limenitis lorquini,*
Nymphalidae	Hesperiidae	Lycaenidae
Danaus plexippus, Agraulis vanilla, Vanessa atalanta, V. cardui, V. anabella, V. virginiensis, Nymphalis antiopa, Junonia coenia, Adelpha californica	*Pholisora catullus*	*Satyrium sylvinus*
Riodinidae		Hesperiidae
Apodemia virgulti, Calephelis nemesis		*Ochlodes agricola*
Lycaenidae		
Strymon melinus, Satyrium tetra, S. saepium, Callophrys augustus, C. dumetorum, Lycaena arota nubila, Brephidium exilis, Leptotes marina, Plebjus acmon, Glaucopsyche lygdamus, Celastrina echo,		
Hesperiidae		
Hylephila phyleus, Ochlodes sylvanoides, Poanes melane, Lerodea eufala, Erynnis tristis, E. funeralis, Pyrgus albescens, Heliopetes ericetorum,		

Only one species, *Papilio cresphontes*, is known to have been absent from Griffith Park historically (specifically around 1900) but is now present

estimate that at least 10 taxa (18 % of the reconstructed historical butterfly community) have been extirpated from the park based on a lack of recent sightings; namely the transect walks but also opportunistic sampling. Note that this is a conservative estimate in that all 10 extirpated species are "confirmed historical" (records from Griffith Park) while several of the species present in the park today (Table S1) could only be identified as "probably historical" (records from areas adjacent to Griffith Park).

Of the 10 extirpated butterfly species in Griffith Park, 6 are from the Nymphalidae family (or 35 % of the historical nymphalid community), 3 from Lycaenidae (23 % of the lycaenids) and 1 Hesperiidae (*Pholisora catullus* Fabricius). We furthermore classified four lycaenids (*Brephidium exilis* Boisduval, *Lycaena arota nubile*, *Satyrium saepium* Boisduval and *S. tetra* Edwards), one hesperid (*Lerodea eufala* Edwards) and one pierid (*Zerene eurydice* Boisduval) as rare in Griffith Park (Table S1). Larval host plant status was a highly significant ($p = 0.003$) predictor of butterfly status while host plant specificity and non-native host plant use were both significant predictors ($p \leq 0.05$) (Table 2). Wingspan was marginally significant alone as a predictor but significant with family as a covariate such that persistent butterfly species tend to be larger than extirpated or rare species (Table 2). The multiple regression models and model averaging generally supported the univariate results such that larval host plant status had the highest relative variable importance followed by specificity, wingspan and non-native host plant use (Table 2).

Discussion

Urbanization early in the twentieth century surrounding Griffith Park appears to have had a rapid and immediate effect on its ecological community. For example, in field notes, Comstock noted seeing the distinctive arrowhead blue *Glaucopsyche piasus sagittigera* Felder & Felder, ("possibly fifty nice fresh ones") on Feb 10, 1917. However, as early as the 1920s *G. piasus sagittigera* was disappearing throughout the L.A basin, and soon afterwards was thought to be entirely extinct here (subsequently, populations have been discovered in the eastern San Gabriel Mountains; see Emmel and Emmel 1973). Other butterfly species were lost more recently, presumably reflecting further degradation of habitat quality through the 1900s as well as from isolation from other populations. One early butterfly collector J.D. Gunder (1930) noted that if you wanted to find Comstock's

Table 2 Results from binomial logistic regressions examining the effect of the predictor variables on butterfly species (*n*) persistence or extirpation/rarity. Regressions were run using only the variable of interest and with family as a covariate. Results from model averaging of multiple logistic regressions is also shown as the relative variable importance (RVI)

Variable	n	Coefficient	Only one variable		Family as a covariate			RVI
			p	Odds ratio	Coefficient	*p*	Odds ratio	
Larval host plant status	46	3.43	0.003	31.00	3.34	0.006	28.33	1.00
Host plant specificity	47	−0.64	0.05	2.00	−0.13	0.04	2.34	0.71
Wing span	49	−0.66	0.08	1.41	−1.67	0.04	2.42	0.51
Non-native host plant use	49	−0.36	0.006	6.12	−0.76	0.01	7.46	0.29
Family	49							
Pieridae		0.13	0.92	1.14				
Lycaenidae		−1.11	0.24	0.33				
Riodinidae		16.31[a]	0.99	–				
Nymphalidae		0.85	0.34	0.43				
Papilionidae		16.31[a]	0.99	–				

[a] Model parameters which did not converge

fritillary *Speyeria callippe comstocki* Gunder, the best place to go was Griffith Park where "many specimens may be taken". Through the 1940s this species was still regularly collected in the park, but today is apparently extirpated from the entire eastern Santa Monica Mountains, including Griffith Park. The checkerspot butterfly *Euphydryas chalcedona* Doubleday was known in the park in the 1950s but no longer occurs, though it may be readily found in late spring in the western Santa Monica Mountains to the west and in the nearby San Gabriel Mountains to the north (TCB, DSC, pers. obs.).

We note that our calculation of loss in Griffith Park butterfly diversity is likely an underestimate of the true loss of biological diversity within the park. First of all, our focus on species presence/absence (historical records of abundance are unreliable) largely neglects declines and contractions of populations of native butterflies that are certain to have taken place in addition to extirpation (Hughes et al. 1997). Second, due to the incomplete historical record, other species, particularly butterfly species, may have been present at one time but not recorded and therefore not known to have been lost. Little is known generally of "pre-American" butterfly communities in California (Shapiro 2009). Some species may also have been lost during the initial settlement of Los Angeles in the nineteenth century. Agricultural and pastoral development of southern California during the 1800s (as opposed to urbanization which was the dominant form of development in the area over our study period in the 1900s) and possibly beforehand likely had large effects on native species but we have no data from that time.

Studies across spatial gradients of urbanization have shown that urban and suburban development can strongly and negatively affect many sensitive butterfly species (Ruszczyk and de Araujo 1992; Blair and Launer 1997; Blair 1999; Clark et al. 2007). Our study supports these findings, but our results also suggest that studies of urbanization spatial gradients alone might be insufficient for assessing urbanization impacts and species extirpation. For example, two species once very common in Griffith Park, *Glaucopsyche piasus sagitigera* and *Pholisora catullus*, vanished from the area during the 1930s, prior to the widespread loss of open space from urbanization. Had we evaluated urban impacts on butterfly diversity simply by comparing species richness along a contemporary east-to-west, urban-to-wildland gradient of the Santa Monica Mountains (and not delved into historical information) we likely would have overlooked these species as having occurred. Historical records can therefore provide critical documentation of conservation threats and reveal historical patterns that might inform future conservation approaches.

We also found that larval host plant status and specificity can exert a strong influence on butterfly extirpation. The close relationship between larval host plant abundance and butterfly persistence status suggests that either (1) the extirpation and (inferred) decline of plants in the park (discussed by Cooper and Mathewson 2009 and Cooper 2011) may have caused coextinction of some of the associated butterflies (Koh et al. 2004) or (2) host plant rarity itself (rather than decline) might be associated with another butterfly trait that makes it vulnerable to extirpation such as metapopulation dynamics (Harrison 1991). Either way, our results corroborate similar studies of butterfly population declines that suggest that habitat degradation (especially host plant displacement via invasive species) can be a devastating threat to persistence of certain sensitive taxa (Schultz and Dlugosch 1999; Weiss 1999; Wagner and Van Driesche 2010). Interestingly, all of the common butterfly species whose hosts are rare (Table S1) are known to accept non-native hosts as well, suggesting that this "ecological flexibility" may be responsible for their persistence. Still, while many Californian butterflies and especially urban butterflies have become reliant upon invasive plants (Shapiro 2002;

Graves and Shapiro 2003) and the ability to use non-native hosts likely aids a butterfly's persistence in Griffith Park, we found non-native host use alone to be of relatively lower importance in predicting persistence (though also significant).

Habitat fragmentation and isolation of the Griffith Park ecosystem due to development surrounding the park (Fig. 1) has also likely contributed to population declines as it has in other butterfly communities (Bergman et al. 2004; Wenzel et al. 2006; Polus et al. 2007). Additional threats such as fire (which can quickly transform native vegetation communities to non-native weeds through "type conversion") and climate change can have compounding effects (e.g. Forister et al. 2010), though we have little or no specific data on these additional impacts. Nor can we distinguish the relative importance of direct (e.g. habitat loss/development) and indirect (e.g. fire) urbanization impacts with the available data.

Still, despite these extinctions and mounting threats in the park there is cause for hope. During the contemporary surveys in 2012 we rediscovered Comstock's own *L. arota nubila* despite its being thought long extirpated in the park (Johnson 2008). Designated as critically imperiled (NatureServe 2011) due to its narrow distribution within highly urbanized southern California, its persistence, albeit a rarity in Griffith Park, emphasizes the urgent need to recognize the conservation value of urban parks (Soga et al. 2014). Indeed, a significant proportion of the butterfly community remains extant in the park (at least 80 % of original), despite essentially no management for biodiversity. Significant populations of rare plants also persist in the park today (Cooper 2011), emphasizing how even urban parks and open spaces can represent effective and valuable conservation reserve systems (Kadlec et al. 2008; Konvicka and Kadlec 2011; Oliver et al. 2011) even when, as is the case for Griffith Park, conservation initiatives have been minimal or slow to develop.

Large patch size of habitat is frequently associated with high species richness and low extinction rates in both bird and butterflies communities in urban areas (Palmer et al. 2008; Gaston 2010; Soga and Koike 2013b), and at 1,700 ha, Griffith Park may have size as an advantage. With the development, and eventual adoption of conservation and management strategies, Griffith Park, and urban parks elsewhere may be able to prevent further ecological deterioration, simply aided by their large size. Most importantly, the extent to which native shrubland ecosystems are recognized as more than "waste land" within urban areas, and are valued for their significant natural resources in the future should help stem ongoing losses of biodiversity in our increasingly urbanized world. For these reasons we look forward to a possible "Hollywood ending" for the wildlife of Los Angeles and other urban centers worldwide.

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References

Bartoń K (2012) MuMIn: multi-model inference. R package version, 1.9.5. http://CRAN.R-project.org/package=MuMIn

Bergman K-O, Askling J, Ekberg O, Ignell H, Wahlman H, Milberg P (2004) Landscape effects on butterfly assemblages in an agricultural region. Ecography 27:619–628

Blair RB (1999) Birds and butterflies along an urban gradient: surrogate taxa for assessing biodiversity. Ecol Appl 9:164–170

Blair RB, Launer AE (1997) Butterfly diversity and human land use: species assemblages along an urban gradient. Biol Conserv 8:113–125

Bonebrake TC, Sorto R (2009) Butterfly (Papilionoidea and Hesperioidea) rapid assessment of a coastal countryside in El Salvador. Trop Conserv Sci 2:34–51

Bonebrake TC, Christensen J, Boggs CL, Ehrlich PR (2010) Population decline assessment, historical baselines, and conservation. Conserv Lett 3:371–378

Brown KS, Freitas AVL (2002) Butterfly communities of urban forest fragments in Campinas, São Paulo, Brazil: structure, instability, environmental correlates, and conservation. J Insect Conserv 6:217–231

Burnham KP, Anderson DR (2002) Model selection and multi-model inference: a practical information-theoretic approach. Springer, New York

Clark PJ, Reed JM, Chew FS (2007) Effects of urbanization on butterfly species richness, guild structure, and rarity. Urban Ecosyst 10:321–337

Comstock JA (1926) Studies in Pacific Coast Lepidoptera (continued). Thirteen new species or aberrations of California butterflies. Bull South Calif Acad Sci 25:29–34

Comstock JA (1927) Butterflies of California: a popular guide to a knowledge of the butterflies of California. Author, Los Angeles

Connor EF, Hafernik J, Levy J, Moore VL, Rickman JK (2002) Insect conservation in an urban biodiversity hotspot: the San Francisco Bay Area. J Insect Conserv 6:247–259

Cooper DS (2011) Rare plants of Griffith Park, Los Angeles. Fremontia 38:18–24

Cooper DS, Mathewson P (2009) Griffith Park wildlife management plan. Unpublished report. Prepared by Cooper Ecological Monitoring, Inc. for the Los Angeles Dept. of Recreation and Parks. 22 January 2009. http://www.griffithparkwildlife.org

Dearborn DC, Kark S (2010) Motivations for conserving urban biodiversity. Conserv Biol 24:432–440

Dures SG, Cumming GS (2010) The confounding influence of homogenising invasive species in a globally endangered and largely urban biome: does habitat quality dominate avian biodiversity? Biol Conserv 143:768–777

Eberts M (1996) Griffith Park: a centennial history. The Historical Society of Southern California

Emmel TC, Emmel JF (1973) The butterflies of southern California. Natural History Museum of Los Angeles County

Fattorini S (2011a) Insect rarity, extinction and conservation in urban Rome (Italy): a 120-year-long study of tenebrionid beetles. Insect Conserv Diver 4:307–315

Fattorini S (2011b) Insect extinction by urbanization: a long term study in Rome. Biol Conserv 144:370–375

Forister ML, McCall AC, Sanders NJ, Fordyce JA, Thorne JH, O'Brien J, Waetjen DP, Shapiro AM (2010) Compounded effects of climate change and habitat shift patterns of butterfly diversity. Proc Natl Acad Sci USA 107:2088–2092

Forister ML, Jahner JP, Casner KL, Wilson JS, Shapiro AM (2011) The race is not to the swift: long-term data reveal pervasive declines in California's low-elevation butterfly fauna. Ecology 92:2222–2235

Garth JS, Tilden JW (1986) California butterflies. University of California Press, Berkeley

Gaston KJ (2010) Urban ecology. Cambridge University Press, Cambridge

Giuliano WM, Accamandon AK, McAdams EJ (2004) Lepidoptera–habitat relationships in urban parks. Urban Ecosyst 7:361–370

Graves SD, Shapiro AM (2003) Exotics as host plants of the California butterfly fauna. Biol Conserv 110:413–433

Grimm NB, Faeth SH, Golubiewski NE, Redman CL, Wu J, Bai X, Briggs JM (2008) Global change and the ecology of cities. Science 319:756–760

Gunder JD (1930) Butterflies of Los Angeles County, California. Bull South Calif Acad Sci 29:1–59

Hardy PB, Dennis RL (1999) The impact of urban development on butterflies within a city region. Biodivers Conserv 8:1261–1279

Harrison S (1991) Local extinction in a metapopulation context: an empirical evaluation. Biol J Linn Soc 42:73–88

Hughes JB, Daily GC, Ehrlich PR (1997) Population diversity: its extent and extinction. Science 278:689–692

Johnson JJ (2008) Butterflies, rarity, and conservation practices. Dissertation UCLA

Jones EL, Leather SR (2012) Invertebrates in urban areas: a review. Eur J Entomol 109:463–478

Kadlec T, Benes J, Jarosik V, Konvicka M (2008) Revisiting urban refuges: changes of butterfly and burnet fauna in Prague reserves over three decades. Landsc Urban Plan 85:1–11

Kattwinkel M, Biedermann R, Kleyer M (2011) Temporary conservation for urban biodiversity. Biol Conserv 144:2335–2343

Koh LP, Sodhi NS (2004) Importance of reserves, fragments and parks for butterfly conservation in a tropical urban landscape. Ecol Appl 14:1695–1708

Koh LP, Sodhi NS, Brook BW (2004) Ecological correlates of extinction proneness in tropical butterflies. Conserv Biol 18:1571–1578

Konvicka M, Kadlec T (2011) How to increase the value of urban areas for butterfly conservation? Eur J Entomol 108:219–229

Kowarik I (2011) Novel urban ecosystems, biodiversity, and conservation. Environ Pollut 159:1974–1983

Lizée MH, Manel S, Mauffrey JF, Tatoni T, Deschamps-Cottin M (2012) Matrix configuration and patch isolation influences override the species–area relationship for urban butterfly communities. Landsc Ecol 27:159–169

Magle SB, Crooks KR (2009) Investigating the distribution of prairie dogs in an urban landscape. Anim Conserv 12:192–203

Magle SB, Hunt VM, Vernon M, Crooks KR (2012) Urban wildlife research: past, present, and future. Biol Conserv 155:23–32

Marzluff JM, Bowman R, Donnelly R (2001) Avian ecology and conservation in an urbanizing world. Kluwer, Norwell

Matteson KC, Langellotto GA (2010) Determinates of inner city butterfly and bee species richness. Urban Ecosyst 13:333–347

McIntyre NE (2000) The ecology of urban arthropods: a review and a call to action. Ann Entomol Soc Am 93:825–835

McKinney ML (2002) Urbanization, biodiversity, and conservation. Bioscience 52:883–890

Natureserve (2011) NatureServe Explorer: an online encyclopedia of life [Online]. www.natureserve.org/explorer

New TR, Sands DPA (2002) Conservation concerns for butterflies in urban areas of Australia. J Insect Conserv 6:207–215

Öckinger E, Dannestam Å, Smith HG (2009) The importance of fragmentation and habitat quality of urban grasslands for butterfly diversity. Landsc Urban Plan 93:31–37

Oliver AJ, Hong-Wa C, Devonshire J, Olea KR, Rivas GF, Gahl MK (2011) Avifauna richness enhanced in large, isolated urban parks. Landsc Urban Plan 102:215–225

Opler PA, Lotts K, Naberhaus T (2013) Butterflies and moths of North America. http://www.butterfliesandmoths.org/(Version September 2013)

Orsak LJ (1977) The butterflies of Orange County, California. Museum of Systematic Biology Research Series no. 4, University of California, Irvine

Palmer GC, Fitzsimons JA, Antos MJ, White JG (2008) Determinants of native avian richness in suburban remnant vegetation: implications for conservation planning. Biol Conserv 141:2329–2341

Pelham JP (2008) A catalogue of the butterflies of the United States and Canada. J Res Lepid 40:1–652

Pellet J (2008) Seasonal variation in detectability of butterflies surveyed with Pollard walks. J Insect Conserv 12:155–162

Pollard E, Yates T (1993) Monitoring butterflies for ecology and conservation. Chapman & Hall, New York

Polus E, Vandewoestijne S, Choutt J, Baguette M (2007) Tracking the effects of one century of habitat loss and fragmentation on calcareous grassland butterfly communities. Biodivers Conserv 16:3423–3436

R Development Core Team (2010) A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna

Ramalho CE, Hobbs RJ (2012) Time for a change: dynamic urban ecology. Trends Ecol Evol 27:179–188

Ramírez Restrepo L, Halffter G (2013) Butterfly diversity in a regional urbanization mosaic in two Mexican cities. Landsc Urban Plan 115:39–48

Ruszczyk A, de Araujo AM (1992) Gradients in butterfly species diversity in an urban area in Brazil. J Lepid Soc 46:255–264

Schultz CB, Dlugosch KM (1999) Nectar and hostplant scarcity limit populations of an endangered Oregon butterfly. Oecologia 119:231–238

Sekar S (2012) A meta-analysis of the traits affecting dispersal ability in butterflies: can wingspan be used as a proxy? J Anim Ecol 81:174–184

Shaffer HB, Fisher RN, Davidson C (1998) The role of natural history collections in documenting species declines. Trends Ecol Evol 13:27–30

Shahabuddin G, Ponte CA (2005) Frugivorous butterfly species in tropical forest fragments: correlates of vulnerability to extinction. Biodivers Conserv 14:1137–1152

Shapiro AM (2002) The Californian urban butterfly fauna is dependent on alien plants. Divers Distrib 8:31–40

Shapiro AM (2009) Revisiting the pre-European butterfly fauna of the Sacramento Valley, California. J Res Lepid 41:31–39

Shochat E, Lerman SB, Anderies JM, Warren PS, Faeth SH, Nilon CH (2010) Invasion, competition, and biodiversity loss in urban ecosystems. Bioscience 60:199–208

Shultz AJ, Tingley MW, Bowie RCK (2012) A century of avian community turnover in an urban green space in Northern California. Condor 114:258–267

Shwartz A, Muratet A, Simon L, Julliard R (2013) Local and management variables outweigh landscape effects in enhancing the diversity of different taxa in a big metropolis. Biol Conserv 157:285–292

Soga M, Koike S (2013a) Patch isolation only matters for specialist butterflies but patch area affects both specialist and generalist species. J For Res 18:1–9

Soga M, Koike S (2013b) Mapping the potential extinction debt of butterflies in a modern city: implications for conservation priorities in urban landscapes. Anim Conserv 16:1–11

Soga M, Yamaura Y, Koike S, Gaston KJ (2014) Woodland remnants as an urban wildlife refuge: a cross-taxonomic assessment. Biodivers Conserv 23:649–659

Swetnam TW, Allen CD, Betancourt JL (1999) Applied historical ecology: using the past to manage for the future. Ecol Appl 9:1189–1206

Trust for Public Land (2010) 2010 City Park Facts. TPL, San Francisco, California. http://www.tpl.org. Accessed Dec 2011)

Wagner DL, Van Driesche RG (2010) Threats posed to rare or endangered insects by invasions of nonnative species. Annu Rev Entomol 55:547–568

Weiss SB (1999) Cars, cows, and checkerspot butterflies: nitrogen deposition and management of nutrient-poor grasslands for a threatened species. Conserv Biol 13:1476–1486

Wenzel M, Schmitt T, Weitzel M, Seitz A (2006) The severe decline of butterflies on western German calcareous grasslands during the last 30 years: a conservation problem. Biol Conserv 128:542–552

Williams MR (2011) Habitat resources, remnant vegetation condition and area determine distribution patterns and abundance of butterflies and day-flying moths in a fragmented urban landscape, south-west Western Australia. J Insect Conserv 15:37–54