Ecological spillover dynamics of organisms from urban to natural landscapes

Jill E. Spear,1,* Erik K. Grijalva,1 Julia S. Michaels,1 and Sophie S. Parker2

1University of California, One Shields Avenue, Davis, CA 95616, USA and 2The Nature Conservancy, 445 South Figueroa Street, Suite 1950, Los Angeles, CA 90071, USA

*Corresponding author. E-mail: jillespear@gmail.com

Submitted: 15 July 2017; Received (in revised form): 5 January 2018; Accepted: 23 February 2018

Abstract

Urbanization and anthropogenic development have fundamentally altered ecosystem dynamics on a global scale. Conservation and management of comparatively less modified landscapes adjacent to highly modified landscapes requires careful consideration of interactions between landscape types. Restoration or conservation of habitat within a developed matrix is generally thought to have beneficial effects on landscape-level ecological processes. We propose an ecological spillover framework to critically assess how restoring or conserving species populations within anthropogenically modified landscapes may affect adjacent wildland populations. Within the framework, the spillover process is divided into seven interconnected ‘nodes’, which identify points at which potential cause-effect relationships may exist between urban and wildland populations. The framework is useful for a wide range of project-specific ecological relationships, and can help scientists and managers identify knowledge gaps and weigh risk in conservation decision-making. We queried the conservation literature to identify research focused on the impacts of urban species populations on regional wildland populations. Our search revealed seven ecological processes that have the potential to be affected by urban to wildland spillover and we found relatively few studies that explicitly analyze spillover effects from urban to wildland areas. Organisms living in urban areas within restored or remnant habitats located in an urban matrix, or within the built environment have largely unknown effects on landscape-level ecological processes. We conclude with a discussion on the critical gaps in research linking these habitats to larger landscape-level ecological understanding, and provide recommendations for research priorities that might illuminate this important aspect of 21st century conservation planning.

Key words: urban, spillover, cities, conservation

Introduction

The practice of maintaining, enhancing and restoring wildlife habitat within highly modified landscapes, such as urban areas, is often aimed at encouraging the growth of native species’ populations, maintaining existing species assemblages and interactions, or providing various ecosystem services. These activities can benefit both people and nature, but conservationists must also consider potential downsides to the preservation of native species in these contexts. Although many populations of native plants and animals—even large mammals—can be found in highly modified environments (Rubin et al. 2002; Spinks et al. 2003; Bland, Tully, and Greenwood 2004; Gehrt 2007), these populations may differ significantly from their counterpart wildland populations in behavior, disease prevalence and genetic makeup among other metrics. Although research has increasingly focused on the biotic and abiotic factors that influence the health and survival of populations in highly modified environments (Gliwicz, Goszczynski and Luniak 1994; McKinney 2002; Hammer et al. 2015), there are few studies that assess the potential of urban populations to impact adjacent wildland populations. The null hypothesis would be...
that populations in urban environments have no influence on the survival, fitness or other ecologic functions of wildland populations, either because the two are isolated from one another, or for some other reason. Lacking information that either supports or refutes the null hypothesis, conservationists working in or near urban landscapes may have a difficult time understanding whether, e.g. an urban environment presents ecological traps (Schlaepfer, Runge and Sherman 2002), or if disease transmission between plants (Poland and Mccullough 2006) or animals (Bradley and Altizer 2007) would be a concern for urban and wildland populations of the species and communities they are working to protect. Because potential negative impacts are species-specific, the overall suitability of an urban environment for the preservation of a native plant or animal population must be assessed on a case-by-case basis (Luniak 2004). Gathering this type of information may create a large research burden for conservation projects focused on urban landscapes, and the resulting list of potential interactions may be difficult to organize and prioritize for additional research and conservation action. A conceptual framework for evaluating these dynamics is therefore a necessary next step in developing robust conservation programs for landscapes in or near urban areas.

To understand the current state of knowledge on spillover dynamics of organisms from urban to natural landscapes, we conducted a comprehensive review of the scientific literature on topics related to urban biodiversity. Using the results of this literature review, we developed a conceptual ecological ‘spillover framework’ to allow for analysis of components of an urban to wildland spillover pathway, occurring between framework ‘nodes’. This allows for the identification of areas of uncertainty in need of further research, and allows for a systematic approach to assess the potential for restoration or conservation activities within a highly modified landscape to impact surrounding wildlands.

In this article, we extend the use of the term ‘spillover’ to specifically denote ecological spillover, which is similar to (and inclusive of) the definitions of spillover used in epidemiology and disease ecology for pathogens [e.g. animal-to-human spillover (Sauvage, Langlais and Pontier 2007; Lloyd-Smith et al. 2009; Flowright et al. 2014, 2017), animal-to-animal (Dobson 2004; Childs, Richt and Mackenzone 2007) and plant-to-plant (Beckstead et al. 2010), see Daszak, Cunningham and Hyatt (2000) for general definition] and in invasive species literature (Meeus et al. 2011; Dunn and Hatcher 2015), but expands the concept to include all potential ecological interactions that result in ecological effects moving from urban to wildland environments.

**Methods**

We conducted an aggregative scoping review (Haddaway and Watson 2016) of the scientific literature databased online within Web of Science Previews and BIOSIS Previews (University of California Davis subscription) on topics related to urban biodiversity from February to May 2015 (Supplementary Fig. S1). We also searched Google Scholar during this same time period to capture relevant articles that may not be included in Web of Science Previews or BIOSIS Previews. We excluded all books, non-empirical studies and gray literature (unpublished material) from our study. The Web of Science database covers journal articles from the year 1900 to the present, and BIOSIS Previews includes articles from 1926 to the present, but due to the relatively recent focus on urban ecological systems in the literature (Shwartz et al. 2014), our results only spanned the last 15 years since 2000 (Velasco et al. 2015).

Prior to starting our search, we created a concept map of relevant search terms grouped into clusters based on overlapping ecological relationships. For example, we clustered the search terms ‘conservation’, ‘genetics’, ‘source/sink’ and ‘inbreeding depression’. For each search term, we tested similar terms and quantified the number of results to ensure that the keywords we selected produced the maximum number of relevant results. For example, the keyword ‘urban’ produced more title search results (97, 220) in BIOSIS Previews than the similar term, ‘city’ (26, 646).

Next, we searched all combinations of cluster terms in all available fields (abstract, title, keywords). We excluded topics related to urban conservation that have been covered extensively by other literature reviews, including invasive species (McKinney 2008), habitat fragmentation (Beninde, Veith and Hochkirch 2015) and agriculture (Queiroz et al. 2014).

Without knowing how much literature had been published to date on the subject, we originally limited geographic scope to California and Mediterranean climates. However, it became immediately very clear that minimal published literature exists and we broadened our geographic scope to include a global distribution. For each cluster of search terms, we first included the keywords ‘California’ or ‘Mediterranean’, then excluded these keywords if they returned no relevant results. We found 4 articles originating from California, 2 for Mediterranean climates outside of California and 23 for other regions.

We conducted a careful filtering process of each paper in our search results to compile a list of citations for final review (Supplementary Fig. S1). First, we read each study title and filtered out irrelevant papers (e.g. papers not related to both urban and wildland populations). Next, we thoroughly read the abstracts of each study, excluding papers that did not focus on the interactions between urban and wildland populations. Finally, from this narrowed set of results, we identified papers specifically related to urban population impacts on wildland populations (rather than wildland population impacts on urban populations) (Table 1). Overall, non-relevant articles fell into one of three categories: (i) articles that indirectly hint at the effects on the broader regional population (e.g. Vandergraaf et al. 2009) without explicitly stating any direct effects, (ii) articles that discuss ecological impacts on urban populations due to urbanization but do not tie this back to effects on the regional population (e.g. Concepcion et al. 2015; Rasner et al. 2015; Stracey and Robinson 2012) or (iii) articles that make a direct comparison between the urban population and the regional population but do not make any linkages as to how the urban population affects the regional population (e.g. Liow, Sodhi and Elmqvist 2001; Partecke and Gwinner 2007; Rubin et al. 2002). The relevant papers were then critically reviewed to determine whether they directly or indirectly addressed the following questions: ‘What types of inter- and intra-specific species interactions exist between urban and wildland populations?’ and ‘Do urban populations have an effect on the larger regional populations of wildland species?’ Our final literature list consisted of 29 total papers (See Table 1).

**Evaluation of the search efficiency**

To evaluate our scope and ensure that we captured all relevant literature, we manually searched all studies cited by the papers that we selected. We also searched the same term clusters on Google Scholar to allow for a search of the broadest selection of...
| Citations            | Relevant framework node | Categories of ecological relationships | Urban area (country)                        | Broad taxonomic groupa | Interaction | Type of test |
|----------------------|--------------------------|----------------------------------------|-------------------------------------------|------------------------|-------------|--------------|
| Dybala et al. (2014) | 1, 2                     | Ecological traps                       | Willows and Los Banos, California (USA)   | Aves, Plantae          | Interspecific | Indirect     |
| Leston and Rodewald (2006) | 1, 2                     |                                         | Columbus, Ohio (USA)                      | Aves, Plantae          | Interspecific | Direct       |
| Mannan, Steidl and Boal (2008) | 1, 2                     |                                         | Tucson, Arizona (USA)                     | Aves, Animal virus     | Interspecific | Direct       |
| Riley, Foley and Chomel (2004) | 1, 2, 3, 4               | Disease transmission                    | San Francisco, California (USA)           | Mammalia               | Interspecific | Direct       |
| Plowright et al. (2011) | 1, 2, 3, 4, 6, 7         |                                         | Brisbane, Rockhampton, Townsville City, & Cairns City (Australia) | Mammalia               | Interspecific | Direct       |
| Fiorello, Noss and Deem (2006) | 1, 2                     |                                         | Various locations (Bolivia)               | Mammalia               | Interspecific | Indirect     |
| Bradley, Gibbs and Altizer (2008) | 1, 2, 3, 4               |                                         | Atlanta, Georgia (USA)                    | Aves, Animal virus     | Interspecific | Direct       |
| Fournier et al. (2014) | 1, 2, 3, 4, 5, 6         |                                         | Natal (Brazil)                            | Mammalia, Protozoa     | Interspecific | Indirect     |
| Goulson Whitehorn and Fowley (2012) | 1, 2                     |                                         | Various locations (Scotland)              | Arthropoda, Protozoa, Mammalia | Interspecific | Indirect     |
| Broadfoot et al. (2001) | 1, 2                     | Novel predator–prey dynamics            | Ontario (Canada)                          | Mammalia               | Interspecific | Direct       |
| Barbar et al. (2015) | 1, 2                     |                                         | San Carlos de Bariloche (Argentina)       | Aves                   | Interspecific | Direct       |
| Malpass, Rodewald and Matthews (2015) | 1, 2                     |                                         | Central Ohio (USA)                        | Aves, Mammalia         | Interspecific | Indirect     |
| Rodewald, Kearns and Shustack (2011) | 1, 2, 3               | Diversity                              | Brisbane (Australia)                      | Aves                   | Interspecific | Indirect     |
| Catterall et al. (2010) | 1, 2, 3                  |                                         | Redon, Dinan, Fougeres, St Malo, Rennes, Angers and Nantes (France); Kemijarvi, Tornio, Kemi, Rovanieme and Oulu (Finland); St Nicholas, Quebec City and Montreal (Canada) | Aves                   | Interspecific | Indirect     |
| Clergeau, Jokimäki and Savard (2001) | 1, 2                     | Demographic changes                    | Munich and Raisting (Germany)             | Aves                   | Interspecific | Indirect     |
| Alternatt (2012)b | 1, 2, 3                  | Phenology                              | Aargau (Switzerland)                      | Arthropoda             | Interspecific | Indirect     |
| Chamberlain et al. (2009) | 1, 2                     |                                         | Various (Various)                         | Aves                   | Interspecific | Indirect     |
| Dominoni et al. (2013) | 1, 2                     |                                         | Munich and Raisting (Germany)             | Aves                   | Interspecific | Indirect     |
| Chiappero et al. (2011) | 1, 2                     | Demographic changes                    | Rio Cuarto (Argentina)                    | Mammalia               | Intraspecific | Indirect     |
| Lehrer, Schooley and Whittington (2012) | 1, 2                     |                                         | Champaign and Urbana, Illinois (USA)      | Mammalia               | Intraspecific | Indirect     |
| Kauffman Frick and Linthicum (2003) | 1, 2, 3                  |                                         | San Francisco and Los Angeles, California (USA) | Aves                   | Intraspecific | Direct       |
| Whelan et al. (2005) | 1, 2, 3, 4               | Genetics/Phenotype                     | Sutherland and Sydney Basin (Australia)    | Plantae                | Intraspecific | Direct       |
| Le Roux et al. (2015) | 1, 2, 3                  |                                         | Various (South Africa)                     | Mammalia               | Intraspecific | Direct       |
| Roy, Butler and Haynie (2013) | 1, 2                     |                                         | Rio Grande Valley, Texas (USA)            | Aves                   | Intraspecific | Direct       |
| Johnson and Galloway (2008) | 1, 2, 3, 4               |                                         | Boyce, Virginia (USA)                     | Plantae                | Intraspecific | Direct       |
| Bjorklund, Ruiz and Senar (2010) | 1, 2, 3                  |                                         | Barcelona (Spain)                         | Aves                   | Intraspecific | Direct       |

(continued)
peer-reviewed journals available. We found only one relevant paper (Dyballa et al. 2014) from peer-reviewed journal Ecological Restoration which is not included in Web of Science BIOSIS database.

**Results**

Out of an initial pool of 1129 research papers from the peer-reviewed literature on urban biodiversity obtained from our search, we identified 29 papers (0.02%) (Supplementary Fig. S1) that inform spillover dynamics from urban to wildland systems (Table 1 and Fig. 1). Because we found only one additional paper that fit our criteria for inclusion using post priori search techniques, it appears that our chosen search terms allowed us to achieve an unbiased reflection of the research literature on urban ecological spillover dynamics. Most research papers we reviewed concentrated on local species dynamics within an urbanized or wildland setting, or on longitudinal studies along an urbanization gradient. The studies fell into eight different categories based on the type of spillover factor (ecological relationship) involved (Table 1). These categories included disease transmission, genetics, source-sink dynamics, demographic changes, ecological traps, novel predator–prey dynamics, phenology and diversity. Two of the papers fell into multiple categories. The number of studies published per year has increased over time, with only 2 years (2002 and 2007) yielding no literature on this topic (Fig. 2). This increase in studies published over time reflects a broader trend in the increase of publications on urban biodiversity more broadly (Magle et al. 2012).

Based on taxonomic data found in Web of Science ISI Web of Knowledge, relevant research papers related to the topic of urban spillover covered only 7 (8.8%) of the 79 high-level (Phyla) taxonomic groups used by (ION) Index to Organism Names (Clarivate Analytics 2009) within the broad groups of Animalia, Microorganisms, Protozoa and Plantae. The 3 groups best represented were Aves (birds) with 16 papers, Plants (Spermatophyta, including Angiospermae and Gymnospermae) with 5 papers, and Mammalia (mammals) with 11 papers (Fig. 3). Papers involving studies of viruses, protozoa and birds were over-represented in our group of 29 papers related to urban spillover, when compared with the conservation literature more broadly, with birds being the most over-represented group. In contrast, plants, invertebrates, reptiles and mammals were under-represented, with plants being the most under-represented group. When we examined the locations where studies related to urban spillover had been conducted, we found that the majority of studies took place in the Northern Hemisphere, with clusters of field sites occurring in northwestern France and northern Finland in Europe. Half (15) of the field sites included locations in North America; the next best represented continents included Europe, with six field locations and South America, with four (Fig. 4).

The largest store of papers elucidating urban to wildland spillover effects was found in the disease transmission literature, with seven papers identifying actual or potential urban to wildland pathways for pathogen transmission (Table 1). Ecological spillover in this context imagines inter- or intra-specific pathogen flow (and potential consequent impacts) from urban populations to wildland populations. Three of these papers specifically address directional transmission (Bradley, Gibbs and Altizer 2008; Broadfoot, Rosatte and O’Leary 2001, Riley, Foley and Chomel 2004), and four indirectly suggest that ecological spillover dynamics are at play (Fournier et al. 2014; Plowright et al. 2011; Fiorello, Noss and Deem 2006; Goulson, Whitehorn, and Fowley 2012).

We found five papers that provide evidence of genetic exchange between urban and wildland populations. A study by Roy, Butler and Haynie (2013) suggests that restored or conserved, yet fragmented, habitat patches within an agricultural or urban context provide sufficient resources to sustain genetically viable populations of the Brownsville common yellowthroat (Geothlypis trichas insperata) in the Lower Rio Grande

| Citations | Relevant framework node | Categories of ecological relationships | Urban area (country) | Broad taxonomic groupa | Interaction | Type of test |
|-----------|-------------------------|----------------------------------------|----------------------|-----------------------|-------------|-------------|
| Roe, Rees and Georges (2011) | 1, 2, 3 | Source-Sink dynamics | Canberra (Australia) | Chordata | Intraspecific | Direct |
| Kauffman, Pollock and Walton (2004) | 1, 2, 3 | | San Francisco and Los Angeles, California (USA) | Aves | Intraspecific | Direct |
| Broadfoot, Rosatte and O’Leary (2001)b | 1, 2 | | Ontario (Canada) | Mammalia | Interspecific | Indirect |
| Padilla and Rodewald (2015) | 1, 2, 3 | | Central Ohio (USA) | Aves | Interspecific | Direct |
| Alternatt (2012)b | 1, 2, 3 | | Aargau (Switzerland) | Arthropoda | Intraspecific | Indirect |

Citation includes details on the publication author and year of publication. Only research-oriented articles were considered for our core results for determining spillover impacts. All synthesis papers and reviews were not included in our core relevant papers that demonstrate spillover effects. Relevant framework nodes column is the number associated with each node of the proposed framework (Fig. 5) discussed within the corresponding research paper according to our proposed framework. Categories of ecological relationships relates to the spillover factors identified in the second node of the proposed framework. The ecological interaction terms are in regards to the context of urban to wildland spillover, which we refer to as ecological spillover factors within our framework. The urban area column is where research was conducted regardless of where the author’s home institution originated and includes urban area or city and country. Taxonomic groupings of organisms covered in the relevant papers are based on ION, Index to Organism Names (Clarivate Analytics 2009) used in BIOSIS. Species interactions are defined as whether the interaction between the urban and wildland population is inter- or intraspecific. Type of test is classified as either ‘Direct’ or ‘Indirect’ as discussed within the relevant paper. Direct test is based on the research within relevant articles that directly test one of the ecological relationships. Indirect test is based on the research within articles that has the potential to provide evidence to support one of the ecological relationship.

aBased on ION, index to organism names (Clarivate Analytics 2009) used in BIOSIS.
bPaper fits into multiple categories and is included in all instances.
Valley of Texas, USA, as fledging individuals maintain little natal site fidelity. Johnson and Galloway (2008) found that the pollen of Lobelia cardinalis was able to travel up to 1 km, suggesting that fertilization of wild plants adjacent to horticultural plantings in urban areas is possible. Finally, Bjorklund, Ruiz and Senar (2010) found that parklands within central Barcelona host great tit (Parus major) populations with a higher degree of genetic diversity than those in adjacent natural habitats, and that gene flow was greater in the urban to wildland direction, but the authors provided no analysis of effects on wildland populations.

We found five studies that examined source-sink dynamics as related to urban spillover. Roe, Rees and Georges (2011) found that urban water sources act as drought refugia for the eastern long-necked turtle (Chelodina longicollis) in Australia, though accessing these desirable urban sites requires individuals from wildland populations to traverse a dangerous urbanized matrix, leading to high mortality and therefore a negative spillover effect on wildland populations. Kauffman, Pollock and Walton (2004) found that coastal populations of peregrine falcons (Falco peregrinus anatum) in southern California preferentially disperse to urban areas, which may act as a pseudo-sink given that the urban areas are used as sources for relocation efforts. Broadfoot, Rosatte and O’Leary (2001) found very dense raccoon (Procyon lotor) and skunk (Mephitis mephitis) populations in Ontario, Canada, where they are subject to increased disease
incidence within this urban environment, and may subsequently transmit disease back to populations in surrounding areas. Padilla and Rodewald (2015) found evidence that urban areas may be acting as sinks for avian species in riparian forests of central Ohio, but that the number and quality of habitat patches within the urban matrix influences longer-term trends in urban populations. In the Swiss canton of Aargau, Altermatt (2012) concluded that urban sites likely serve as sinks for butterflies within the overall habitat matrix, drawing immigrants from adjacent, higher-quality habitats.

Our search identified three papers that touch on demographic changes in urban populations relative to wildland populations. All three studies found that urban populations of species have higher survival rates, particularly during the winter or inactive season, than do conspecific populations outside of urban areas. Two of the papers (Lehrer, Schooley and Whittington 2012; Chiappero et al. 2011) address spillover indirectly, whereas one paper (Kauffman, Frick and Linthicum 2003) specifically examines spillover from urban to peri-urban habitats. Chiappero et al. (2011) examined population genetic structure in urban and peri-urban rodents (Calomys musculinus) in Cordoba, Argentina and found that there were significant demographic differences between the two populations. Specifically, the non-urban populations have greater annual demographic fluctuation in the form of higher turnover than that of their urban counterparts. Most wild individuals die each year and are replaced the subsequent season by mixing of a small pool of overwintering adults, whereas in urban settings, perhaps owing to the heat island effect of cities, rodent populations have greater winter survival. Although there may be sufficient demographic plasticity in this species to preclude urban to wildland spillover, under our framework, reduced winter cull (selection) in urban settings could produce genotypes that are maladaptive to wild habitats.

Lehrer, Schooley and Whittington (2012) found that there were no differences in survivorship between urban and non-urban populations of woodchucks (Marmota monax) during the active season, but survival rates were higher for woodchucks in urban environments during the inactive season. Since a significant amount of mortality in rural woodchucks comes in the inactive season where hibernating woodchucks have insufficient fat stores to survive the winter cold, the subsidy effect of urban areas (either via heat island effect during winter or additional foraging opportunities during the active season) could also result in maladaptive traits to spill over into wild populations. Cause-specific mortality during the active season differed as well. Natural predators dominated cause of death in rural settings, whereas in urban settings vehicles constituted the largest cause of death for woodchucks. This points to different selection pressures at work on the two populations, and could result also result in spillover of maladaptive traits. Both of the
previous examples only suggest a potential for ecological spillover. However, Kauffman, Frick and Linthicum (2003) conclude that observed overall increases in the peregrine falcon population of rural habitats is not supported by the intrinsic growth rate of birds in this habitat, and is instead a result of immigration from urban dispersers.

We found three papers that address urban to wildland spillover effects within the context of ecological traps (Lejost and Rodewald 2006; Mannan, Steidl and Boal 2008; Dybala et al. 2014). Ecological traps describe habitats within a heterogeneous habitat matrix that have lower fitness for focal species despite having similar per capita resources when compared with similar habitats (Robertson and Hutto 2006). They are habitats where reproduction and survival are insufficient to support a population despite provision of sufficient resources to attract immigration from regional population sources, and which are chosen over other high-quality habitats that would support sustainable populations (Battin 2004). Each of the papers we found examined the potential for urban areas to function as traps for the larger surrounding wildland matrix. Two of the studies directly tested ecological trap dynamics (Lejost and Rodewald 2006; Mannan et al. 2008), and one was a literature review and data synthesis paper (Dybala et al. 2014).

We also found three papers focused on novel predator-prey dynamics (Rodewald et al. 2011; Barbar et al. 2015; Malpass, Rodewald and Matthews 2015). Urbanized environments significantly alter trophic interactions in many ways, including winnowing species pools to generalist organisms capable of surviving in highly modified habitats subject to high disturbance, resource subsidies, modified foraging dynamics, dispersal and other changes (Chace and Walsh 2006; McKinney 2006). The three papers, all focused on birds whose dispersal capabilities allow for potential movement between urban and wildland environments, explored whether changes in trophic interactions spill over into adjacent wildland areas.

Our search revealed three papers that indirectly address phenological changes related to animals (butterflies and birds) and the potential for these changes to spill over into nominally unaltered wildland settings. Alternatt (2012) describes the potential for spillover when urban-induced phenological shifts are maladaptive to wildland settings, or when phenologically isolated populations develop. Chamberlain et al. (2009) and Dominoni et al. (2013) discuss temporal differences in behavior between urban and rural populations of bird species, suggesting that these differences may potentially decrease the effective regional population size and genetic pool and the potential for incipient allopatric speciation.

Finally, we encountered two papers (Clergeau, Jokimaki and Savard 2001; Catterall et al. 2010) that examined the potential for spillover in the context of diversity. Species diversity in urban settings, (i.e. species richness and species abundance) can vary according to the particular urban setting studied, but is very often equal to or greater than the diversity found in adjacent wildland settings (McKinney 2002, 2006). This is due to the influx of non-native global generalists via accidental or intentional introductions which replace native specialists unable to tolerate modified human ecology in the developed setting. Spillover effects may occur where urban taxa are functionally or phylogenetically related to taxa in surrounding wildlands, impacting native ecology. The two papers we found only inferred that potential spillover effects exist; none made direct tests of these effects.

Discussion

There are shortcomings in the literature when considering the effects of urban species populations on wildland species populations. Many articles we found seemed to be good candidates to discuss spillover dynamics in urban systems. However, upon further analysis, the articles stopped short of linking the effects of the urban population to the regional population (spillover) (see ‘Methods’ section). We also discovered that for this topic, coverage of both taxonomic groups and geographic locations is limited. The taxonomic bias seen within the general conservation literature (Clark and May 2002; Shwartz et al. 2014; Velasco et al. 2015) is reflected in the research published on spillover dynamics in urban systems, with birds, plants and mammals receiving the most attention (Fig. 3). Similarly, we found that the geographic bias present in the general conservation literature (Lawler et al. 2006; Griffiths and Dos Santos 2012; Shwartz et al. 2014), was present for non-global spillover-relevant studies as well, as these were primarily performed in North America, Europe and South America (Fig. 4), with Australia a close fourth.

We propose an ecological ‘spillover framework’ (Fig. 5) to allow for analysis of components of an urban to wildland spillover pathway, occurring between framework ‘nodes’ (henceforth, nodes) to identify areas of uncertainty in need of further research. Each node can represent a discrete opportunity to engage with the relevant research on the subject as well as to consider site-specific details pertinent to spillover potential in a particular case study. Considered separately, individual nodes of the spillover framework may not necessarily indicate realized spillover, since it is mainly the connection and interaction between nodes that leads to realized spillover effects.

The framework nodes are arranged to allow an analysis to move from an urban landscape toward an adjacent or surrounding wildland landscape. This unidirectionality is an assumed premise, developed with the understanding that all nodes are interconnected and that the spillover process may move in both directions simultaneously. The framework seeks to identify ‘net’ spillover effect, and, equally importantly, gaps in knowledge that preclude assessment of spillover effects in restoration and conservation projects. Net spillover may be positive, negative or neutral in terms of effect size, but this assessment is not meant to connote a subjective value of the spillover effect that transcends the context of the particular intervention under consideration. For example, if increased fecundity of native species X within a restored habitat patch in an urban setting results in increased emigration to surrounding wildlands, this may represent a positive effect on the wildland population of species X; an increase, in absolute terms. However, whether or not this population increase in the wildland setting is ‘good’ (or positive, in the subjective sense) is a valuation anchored solely in the goals of the intervention. This spillover framework aims to provide a tool for understanding what quantitative analysis of spillover is possible, where resources can be allocated to illuminate areas of uncertainty, and subsequent assessments of risk relevant to restoration and conservation planning.

Recently, Flowlrigh et al. (2017) proposed a detailed synthetic framework for assessing zoonotic spillover potential (animal-to-human transmission). This framework incorporates the rich research history in epidemiology and disease ecology into an interacting hierarchy of spillover pathways and bottlenecks to understand gaps in knowledge, determine the parameters of risk analysis, examine potential points of intervention and control, and develop mathematical models for zoonotic spillover,
among other goals. We share these goals in our framework for ecological spillover from urban to wildland ecosystems in terms of restoration or conservation activities across those habitat types.

There are several parallels in this zoonotic spillover framework and the framework we propose for ecological spillover. This is especially true for the cases we present of pathogens moving between the urban matrix and wildlands. The detailed synthesis presented by Plowright et al. (2017) is exactly the kind of analysis required for the (non-pathogen) factors we propose in our framework. Thus, the framework as proposed by Plowright et al. (2017) is nested within the larger framework of ecological spillover, especially as relates to the factors identified that precede human exposure to pathogens. Under our ecological spillover framework, then, a generic pathogen would pass through all nodes as identified in Figure 5 (conforming to our conceptual framework), while also conforming to the more detailed framework proposed by Plowright et al. (2017).

In the ecological spillover framework, the first node is the ‘focal construct’. Conservationists and restoration practitioners may be concerned with spillover effects between populations of a particular threatened or endangered species (intra-specific interactions), or between communities of multiple interacting species (inter-specific interactions). Managers may also be interested in spillover effects on an ecosystem process or service, such as pollination. Clear identification of the focal construct allows for assessment of what is known about that subject, and serves to concentrate efforts on understanding potential spatial and temporal interactions that may be relevant in terms of spillover. For example, analyzing potential intra-specific spillover would differ from inter-specific spillover effects (i.e. trophic disruptions), and would therefore require a tailored literature review relevant to the case at hand.

Once a focal construct is defined, the next step in the spillover framework is to analyze a ‘spillover factor’ relevant to the intervention in question (Fig. 5). We have identified several potential spillover factors, defined as potentially quantifiable modifications to both urban and wildland environments that are likely to alter existing ecological relationships. Additional project-specific factors may be more relevant to individual interventions. Spillover factors may include incidence of specific diseases, modifications to trophic dynamics, intra-specific competition, phenological changes, genetic changes at the population level, or other factors. As in defining the focal construct, determining the scope of knowledge of the spillover factor and identification of gaps is key for this node in the spillover framework.

The next node in the framework, ‘conveyance’, relates to ecological conditions necessary for a spillover factor to transfer from an urban to a wildland setting. For example, differences in phenology between urban and wildland populations may reduce interaction between these two populations, preventing the conveyance of a potential spillover factor. It is therefore important to determine the dispersal ability of a given spillover effect, the vectors available (roads, air-travel with birds or insects, parasitism etc.), and the spatial arrangement of barriers, buffers and connectivity.

‘Acquisition’, ‘establishment’ and ‘spread’ are the next nodes in the framework. Once a spillover is conveyed to a recipient wildland environment, the subject wildland population must be susceptible to acquiring the spillover effect or may exhibit resistance or resilience to acquiring the change. Establishment allows for a gestation within the new wildland environment, wherein the spillover factor persists, and either immediately or following a lag, spreads in the new wildland population, beyond the initial area of acquisition.

Finally, there must be a quantifiable ‘effect’ size in the spillover factor in question, defined as a change to the previous wildland state associated with spillover once it has been acquired, become established, and subsequently spread. In the
case of a regional restoration program goal of increasing the fitness of a wildland population of a given species, a quantifiable reduction in fitness of the wildland population as a result of spillover, would indicate a negative spillover effect. If there is a quantifiable increase in the fitness of the wildland population as a result of spillover, then it can be said that the spillover effect is considered positive. Finally, if there is no quantifiable change in the fitness of the wildland population as a result of spillover, then it can be said that the spillover effect is neutral. This is different from saying that there was no spillover effect, because the spillover effect has been acquired, has established, and has spread. For example, if the spillover factor is a disease that only targets individuals that are past reproductive age, there may be no net effect on overall population fitness.

Our review of the literature found that eight different types of ecological relationships can be affected by urban to wildland spillover, including disease transmission, genetics, source-sink dynamics, demographic changes, ecological traps, novel predator–prey dynamics, phenology and diversity. However, we found no examples of papers that give these relationships a full analysis under this spillover framework. In one instance, Blitzer et al. (2012) analyzed the literature to identify research into spillover from agricultural landscapes to ‘natural’ landscapes, finding very few studies that make that explicit directional link. Oro et al. (2013) summarize examples of food subsidy in urban environments that result in morphological and behavioral changes to carnivores that may result in changes to gene frequency. As carnivores can have large foraging and reproductive home ranges (even in the case of a reliable subsidy), there is potential for genetic exchange between urban and wildland populations with unknown effects. We submit that the analysis of both urban and agricultural spillover can be approached with the spillover framework described earlier. As an example of how the spillover framework can be applied, Plowright et al. (2011) used a simulation-based modeling study to examine the transmission dynamics of Hendra virus from flying foxes (Pteropus spp.) in Australia to horses and humans. Viewing this study within our proposed framework, the ‘urban focal construct’ (Node 1) is Pteropus spp, and the ‘spillover factor’ (Node 2) is Hendra virus. The authors tested both urban and rural populations of flying foxes and showed that urban populations of flying fox had much higher rates of infection than their rural counterparts. The authors state that ‘conveyance’ (Node 3) of Hendra virus is dependent on migration, which, in urban populations, has been significantly reduced due to a behavioral adaptation called “urban habitation.” This reduction in migration behavior (Node 3) has led to increased concentration of the disease within urban areas, but reduced acquisition, establishment, and spread (Nodes 4–6) to adjacent flying fox populations. Therefore, based on this simulation, while urban flying fox populations pose great risk of infection to horse and human populations in urban areas, reduced migration dampens the risk of this infection spilling over into wildland flying fox populations (Node 6) and leading to outbreaks of the disease in other wildland species (Nodes 7 and 8).

Although there may be a sizable literature on any one of these individual steps, as one moves through the spillover framework from urban to wildland populations, no studies explicitly link all framework nodes, though two studies allow for inference of spillover dynamics at work across all nodes (Catterall et al. 2010; Fournier et al. 2014) (see Table 1). As a result, we found no articles that discuss urban to wildland spillover directly. This result is mirrored by that found by Blitzer et al. (2012) who examined spillover from managed (agricultural) to natural systems. In that study, the authors reviewed evidence for spillover within five functional groups (herbivores, pathogens, pollinators, predators and seed dispersers) and found less than five studies per group that examined managed to natural spillover directionality. In this study, Blitzer et al. (2012) conclude, “We find that studies of spillover from managed to natural systems have been generally underrepresented relative to those examining flow in the opposite direction.”

Conclusions and recommendations

With urbanization increasing globally, urban environments are becoming more important with regards to conservation strategies. Fazey, Fischer and Lindenmayer (2005) concluded that only 10% of the conservation literature occurs in patchy environments with small and large fragments such as urban–rural systems while 45% of conservation research is occurring in natural areas, and the remaining 45% of research is occurring in small fragments (12%), large fragments (7%), multiple areas (22%) and islands (4.4%). Recently, there have been more studies focused on urban biodiversity conservation, but there are large gaps in our knowledge base on urban conservation research generally (Shwartz et al. 2014), and on spillover dynamics of urban systems more specifically, as we uncovered in our review. Therefore, importance should be placed on understanding how urban species populations can affect the broader regional population of a species through inter- and intra-specific interactions.

Recent urban research has focused on disease transmission, genetics, and source-sink dynamics; the categories of research that elicited the greatest number of results in our review. Going forward, research on demographic changes, ecological traps, predator–prey dynamics, phenology and ecosystem services with regard to spillover dynamics in urban systems should be conducted to augment understanding of spillover as proposed by our framework. Our work found limited taxonomic and geographic coverage, and we recommend researchers diversify studies by including other taxonomic groups and geographic locations not well represented in the literature that may have particular ecological relevance for study sites in terms of spillover. Future research should also include examinations of regional and landscape scale factors. Fazey, Fischer and Lindenmayer (2005) found that local-scale research dominated the literature at 66%, whereas landscape-scale research made up 23%, and regional-scale research comprised just 12% of the literature. Spillover dynamics from urban to regional wildland populations are happening on a landscape or regional scale (Shwartz et al. 2014), and larger spatial scales are necessary to include both urban and rural species populations and their combined interactions. As such, new efforts should focus on impacts occurring at a larger scale.

Moving forward, our recommendations for policy-makers, planners, and land managers are multifaceted. First, one must consider inter- and intra-specific interactions between the urban population and the regional population. In many cases, the two populations do not exist in isolation and there is a permeable barrier in both directions for species to interact (Fig. 5). Our analysis clearly shows that interactions are occurring between these two urban and wildland populations. Whether the net spillover effect between these populations is positive, negative or neutral, the species interactions should be accounted for in management and policy decisions. Second, there is little research on spillover dynamics, and those tasked with responsibilities in conservation or restoration...
management should build their own specific framework tailored to the species, urban system(s) of concern, surrounding wildland and project goals. The framework nodes can then serve as topical benchmarks to examine the existing literature for previously documented effects relevant to the conservation action. Further, this initial literature review can illuminate gaps in existing research about the spillover system, and point to areas of study that will fill in unknown components and determine linkages within the framework.

The proposed framework builds upon established research of urban systems and is helpful in identifying knowledge gaps and understanding the relevant processes and interactions within the urban and wildland setting. Studies that compare urban systems to rural systems are a first step in the process of acquiring information that helps complete our proposed spillover framework while quantifying how urban and wildland populations of species are different reveals new knowledge useful for structuring a study to look at spillover dynamics between the two systems. As suggested by Shochat et al. (2006), human activities that alter both ecological and evolutionary processes require a balance between descriptive and experimental ecology. We agree, and suggest that this inclusiveness also applies to the investigation of spillover dynamics, because both descriptive ecology and experimental ecological research are needed to make linkages in the framework and shed light on inter- and intra-specific interactions between urban and wildland systems. Descriptive ecology can help quantify how urban and rural populations are different and what linkages may exist, while experimental ecology allows researchers to manipulate variables to test for effects. Both methods can be instrumental in overcoming the challenge of elucidating spillover dynamics, as conservation efforts in urban systems and their nearby hinterlands proceed.

**Supplementary data**

Supplementary data are available at JUECOL online.

**Acknowledgements**

We would also like to thank Rodd Kelsey at The Nature Conservancy, and Mark Schwartz at the University of California, Davis, for their advice in the development of this research idea. Another thank you goes to Mary Cadenasso and her laboratory at University of California, Davis for reviewing an early draft of this manuscript and providing commentary.

**Funding**

The authors would like to acknowledge The Nature Conservancy’s Greater Los Angeles Urban Conservation Program for providing funding that supported this research.

**Conflict of interest statement.** None declared.

**References**

Alttermatt, F. (2012) ‘Temperature-Related Shifts in Butterfly Phenology Depend on the Habitat’, Global Change Biology, 18: 2429–38.

Barbar, F. et al. (2015) ‘Emerging Ecosystems Change the Spatial Distribution of Top Carnivores Even in Poorly Populated Areas’, PloS One, 10: e0118851.

Battin, J. (2004) ‘When Good Animals Love Bad Habitats: Ecological Traps and the Conservation of Animal Populations’, Conservation Biology, 18: 1482–91.

Beckstead, J. et al. (2010) ‘Cheatgrass Facilitates Spillover of a Seed Bank Pathogen onto Native Grass Species’, Journal of Ecology, 98: 168–77.

Benin de, J., Veith, M., and Hochkirch, A. (2015) ‘Biodiversity in Cities Needs Space: A Meta-Analysis of Factors Determining Intra-Urban Biodiversity Variation’, Ecology Letters, 18: 581–92.

Bjorklund, M., Ruiz, I., and Senar, J. C. (2010) ‘Genetic Differentiation in the Urban Habitat: The Great Tits (Parus Major) of the Parks of Barcelona City’, Biological Journal of the Linnean Society, 99: 9–19.

Bland, R. L., Tully, J., and Greenwood, J. J. D. (2004) ‘Birds Breeding in British Gardens: An Underestimated Population?: Capsule More Birds Breed in Gardens than Previous Estimates Suggest’, Bird Study, 51: 97–106.

Blitzer, E. J. et al. (2012) ‘Spillover of Functionally Important Organisms between Managed and Natural Habitats’, Agriculture, Ecosystems and Environment, 146: 34–43.

Bradley, C. A., and Altizer, S. (2007) ‘Urbanization and the Ecology of Wildlife Diseases’, Trends in Ecology and Evolution, 22: 95–102.

——, Gibbs, S. E. J., and Altizer, S. (2008) ‘Urban Land Use Predicts West Nile Virus Exposure in Songbirds’, Ecological Applications, 18: 1083–92.

Broadfoot, J. D., Rosatte, R. C., and O’Leary, D. T. (2001) ‘Raccoon and Skunk Population Models for Urban Disease Control Planning in Ontario, Canada’, Ecological Applications, 11: 295–303.

Catterall, C. P. et al. (2010) ‘Long-Term Dynamics of Bird Diversity in Forest and Suburb: Decay, Turnover or Homogenization?’, Diversity and Distributions, 16: 559–70.

Chace, J. F., and Walsh, J. J. (2006) ‘Urban Effects on Native Avifauna: A Review’, Landscape and Urban Planning, 74: 46–69.

Chamberlain, D. E. et al. (2009) ‘Avian Productivity in Urban Landscapes: A Review and Meta-Analysis’, ibid, 151: 1–18.

Chiappero, M. B. et al. (2011) ‘Contrasting Genetic Structure of Urban and Rural Populations of the Wild Rodent Calomys Musculinus (Cricetidae, Sigmodontinae)’, Mammalian Biology, 76: 41–50.

Childs, J. E., Richt, J. A., and Mackenzie, J. S. (2007) ‘Introduction: Conceptualizing and Partitioning the Emergence Process of Zoonotic Viruses from Wildlife to Humans’, Wildlife and Emerging Zoonotic Diseases: The Biology, Circumstances and Consequences of Cross-Species Transmission, 315: 1–31.

Clarivate Analytics. 2009. Index to Organism Names. World Wide Web electronic resource. <www.organismnames.com> accessed November 2017.

Clark, J. A., and May, R. M. (2002) ‘Taxonomic Bias in Conservation Research’, Science, 297: 191–2.

Clereguet, P., Jokimäki, J., and Savard, J.-P. L. (2001) ‘Are Urban Bird Communities Influenced by the Bird Diversity of Adjacent Landscapes?’, Journal of Applied Ecology, 38: 1122–34.

Concepción, E. D. et al. 2015. Impacts of urbanisation on biodiversity: the role of species mobility, degree of specialisation and spatial scale. Oikos, 124: 1571–82.

Daszak, P., Cunningham, A. A., and Hyatt, A. D. (2000) ‘Wildlife Ecology—Emerging Infectious Diseases of Wildlife—Threats to Biodiversity and Human Health’, Science, 287: 443–9.

Dobson, A. (2004) ‘Population Dynamics of Pathogens with Multiple Host Species’, American Naturalist, 164: S64–78.

Dominoni, D. M. et al. (2013) ‘Clocks for the City: Circadian Differences between Forest and City Songbirds’, Proceedings of the Royal Society B, 280: 20130593.
Fragmented Landscape’, The Wilson Journal of Ornithology, 125: 402–6.
Rubin, E. S. et al. (2002) ‘Bighorn Sheep Habitat Use and Selection near an Urban Environment’, Biological Conservation, 104: 251–63.
Sauvage, F., Langlais, M., and Pontier, D. (2007) ‘Predicting the Emergence of Human hantavirus Disease Using a Combination of Viral Dynamics and Rodent Demographic Patterns’, Epidemiology and Infection, 135: 46–56.
Schlaepfer, M. A., Runge, M. C., and Sherman, P. W. (2002) ‘Ecological and Evolutionary Traps’, Trends in Ecology and Evolution, 17: 474–80.
Shochat, E. et al. (2006) ‘From Patterns to Emerging Processes in Mechanistic Urban Ecology’, Trends in Ecology and Evolution, 21: 186–91.
Shwartz, A. et al. (2014) ‘Outstanding Challenges for Urban Conservation Research and Action’, Global Environmental Change, 28: 39–49.
Spinks, P. Q. et al. (2003) ‘Survival of the Western Pond Turtle (Emys Marmorata) in an Urban California Environment’, Biological Conservation, 113: 257–67.
Stracey, C. M., and Robinson, S. K. (2012) ‘Are Urban Habitats Ecological Traps for a Native Songbird? Season-Long Productivity, Apparent Survival, and Site Fidelity in Urban and Rural Habitats’, Journal of Avian Biology, 43: 50–60.
Vandergast, A. G. et al. (2009) ‘Loss of Genetic Connectivity and Diversity in Urban Microreserves in a Southern California Endemic Jerusalem Cricket (Orthoptera: Stenopelmatidae: Stenopelmatus n. sp. “Santa Monica”)’, Journal of Insect Conservation, 13: 329–45.
Velasco, D. et al. (2015) ‘Biodiversity Conservation Research Challenges in the 21st Century: A Review of Publishing Trends in 2000 and 2011’, Environmental Science and Policy, 54: 90–6.
Whelan, R. J. et al. (2005) ‘The Potential for Genetic Contamination vs. Augmentation by Native Plants in Urban Gardens’, Biological Conservation, 128: 493–500.