Existing ecological theory applies to urban environments

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Abstract

There is a prominent view within urban ecology that existing ecological theory is insufficient to understand the ecology of urban environments. However, many ecological theories, hypotheses and paradigms have been shown to apply to cities just as they do to other types of ecosystems. Here, I identify 16 ecological theories that have been applied to urban environments, with examples. I also illustrate the utility of metapopulation theory in cities with a case study on pond-breeding frogs in Melbourne, Australia.

Keywords Amphibians · Cities · Frogs · Urban ecology · Metapopulation theory

Introduction

A prominent school of thought within urban ecology holds that existing ecological theory is insufficient to understand the ecology of cities, where natural systems and human systems intersect (e.g., Alberti 2008; McPhearson et al. 2016). It has been proposed that urban ecosystems are more complex than other types of ecosystems because of their dynamism, their heterogeneity (across multiple spatial and temporal scales), their nonlinearity, the presence of social–biophysical feedbacks in cities, and the varied actions of thousands or millions of resident humans (Andersson 2006; Alberti 2008; Pickett et al. 2008; Qureshi et al. 2014). However, many other ecosystems are dynamic and heterogeneous, with various properties and transitional states that do not follow linear trajectories (e.g., Levin 1998; Anand et al. 2010). The complexity of multiple variables operating simultaneously across diverse spatial and temporal scales can be observed in a range of terrestrial, freshwater and marine ecosystems (e.g., Boit et al. 2012; Bozec et al. 2013; Laurance et al. 2014). Further, every ecosystem on Earth is now influenced in some way by the actions of humans, even if these actions are distant in space or time (e.g., Jambeck et al. 2015; Obrist et al. 2017).

I have previously argued that urban ecosystems, while displaying certain unique properties, do not have a unique ecology; that the apparent novelty of urban ecosystems does not translate into the need for a novel ecological theory to understand their structure and function (Parris 2016; also see Niemelä 1999; Catterall 2009; Faeth et al. 2011). For example, population dynamics in urban environments are governed by the same processes of birth, death, immigration and emigration as populations in other types of environments, while ecological communities in cities are shaped by the same processes of selection, dispersal, ecological drift and evolutionary diversification (Vellend 2010) that operate in woodlands, grasslands, lakes, estuaries and oceans. Despite the disruptions caused by the construction and operation of infrastructure such as houses, factories, roads, pavements, street lights and stormwater drains, urban ecosystems still function to cycle carbon, water and nutrients, and to provide services such as primary production, absorption of atmospheric pollutants, shading, cooling and the treatment of waste products (Parris 2016). To support this argument, I highlight here a range of ecological theories known to apply to urban environments. I also illustrate the utility of metapopulation theory in cities with a case study on pond-breeding frogs in Melbourne, Australia.

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Ecological theories, hypotheses and paradigms

A wide diversity of ecological theories, hypotheses and paradigms have been shown to apply to urban ecosystems (Table 1). These include niche theory and its many applications [such as species distribution models, trait-based analyses and studies of the temporal or spatial partitioning of resources within an ecological community (Parris 2016)]; the gradient paradigm of Whittaker (1967) in its manifestation as the urban–rural gradient of McDonnell and Pickett (1990); and the theory of landscape ecology including the concepts of habitat fragmentation, habitat isolation, and the patch–matrix model identifying areas

of habitat and non-habitat in a landscape. Metapopulation and metacommunity theory, neutral theory, ecological trap theory and predator–prey dynamics, as well as behavioural ecology theories such as the acoustic adaptation hypothesis and optimal foraging theory, also have demonstrated utility in urban environments (Table 1). For example, a series of studies in Melbourne, Australia has applied the gradient paradigm, niche theory, metapopulation theory, metacommunity theory, landscape theory, the acoustic adaptation hypothesis, predator–prey relationships and the epidemiology of wildlife diseases to understand the ecology of pond-breeding frogs across the city (Parris 2006; Parris et al. 2009; Hamer and Parris 2011, 2013; Heard et al. 2013, 2015).

Table 1 A selection of ecological theories, paradigms and hypotheses that have been applied to urban environments, with some examples; please note that this list is not exhaustive

Theory and key reference(s)	Study system	References
Acoustic adaptation hypothesis (Morton 1975)	Birds, frogs, insects	Brumm and Slabbekoorn (2005), Parris et al. (2009) and Lampe et al. (2014)
Ecological trap theory (Dwernychuk and Boag 1972)	Aquatic insects, urban wetlands	Horváth et al. (2009) and Hale et al. (2015)
Host-pathogen dynamics in a metapopulation (Thrall and Burdon 1997)	Amphibians and chytridiomycosis	Heard et al. (2014, 2015)
Food webs/trophic dynamics (Hairston et al. 1960)	Phoenix, Arizona; Sunshine Coast, Australia	Faeth et al. (2005) and Huijbers et al. (2013)
General theory of ecological communities (Vellend 2010)	Microbes in wastewater	Nemergut et al. (2013)
Gradient paradigm (Whittaker 1967)	Fungi, plants, birds, mammals, fish, insects	McDonnell and Pickett (1990), Ishitani et al. (2003) and McDonnell and Hahs (2008)
Intermediate disturbance hypothesis (Connell 1978)	Birds, butterflies, plants, millipedes	Blair (1996), McKinney (2008) and Bogyó et al. (2015)
Interspecific (resource) competition (Tansley 1917)	Birds, mosquitoes	Shochat et al. (2010) and Rochlin et al. (2013)
Landscape theory (Naveh and Lieberman 1984)	Urban landscapes, grasslands, insects	Luck and Wu (2002), Williams et al. (2005) and Muñoz et al. (2015)
Mesopredator release (Soulé et al. 1988)	Coastal California, urban and peri-urban parks in Virginia	Lewis et al. (1999) and Chupp et al. (2013)
Metapopulation theory (Levins 1969)	Reptiles, amphibians	Mollov and Volkonova (2009) and Heard et al. (2013)
Metacommunity theory (Gilpin and Hanski 1991; Leibold et al. 2004)	Amphibians, reptiles, aquatic invertebrates	Parris (2006) and Johnson et al. (2013)
Neutral theory of biodiversity and biogeography (Hubbell 2001)	Birds	Sol et al. (2014)
Niche theory (Grinnell 1917; Hutchinson 1957)	Molluscs, plants, bats, reptiles, arthropods, amphibians	Baur and Baur (1993), Parris and Hazell (2005), Armstrong (2009), Duncan et al. (2011) and Wilson et al. (2013)
Optimal foraging theory (Charnov 1976)	Squirrels, birds, lizards	Bowers and Breland (1996), Shochat et al. (2004) and Chejanovski et al. (2017)
Predator–prey dynamics (Lotka 1925; Volterra 1926)	Birds and nest predators, tadpoles and fish	Rodewald et al. (2011) and Hamer and Parris (2013)

Case study: pond-breeding frogs in Melbourne, Australia

Here, I assess the relative influence of metapopulation processes and local habitat features on the persistence of four species of frogs in 104 ponds across the Melbourne metropolitan area. A metapopulation can be defined as a group of discrete populations, each occupying a separate patch of habitat, but with some level of dispersal between them. Over time, each patch of habitat may be occupied or unoccupied, as existing populations go locally extinct and empty patches are colonized by individuals that establish new populations; these changes are known as metapopulation dynamics (Hanski 1994a, b). Metapopulation theory (Levins 1969) proposes that small patches of habitat are less likely to support a population than large patches because of a higher probability of local extinction, while isolated patches are less likely to support a population than patches close to other suitable habitat because of a lower probability of colonization (immigration) from another patch (Hanski 1994a, 1999). Thus, the size and connectedness of habitat patches are important drivers of metapopulation dynamics. However, environmental conditions within each patch also play a role in the persistence of populations and the likelihood of colonization, as determined by the ecological niche and resource requirements of the species in question (Hanski 1999).

In this case study, I consider each pond to be a habitat patch which at any one time may or may not support a population of each target frog species. Using logistic regression modeling in a Bayesian framework, I assess the relative importance of pond size and connectedness (as proxies for metapopulation processes) and certain habitat characteristics of each pond (as indicators of species-environment or niche relationships) for the occupancy of a pond by each species. Degradation of aquatic habitats with urbanization may lead to the loss or inaccessibility of key resources for wildlife (Parris 2016); for example, urban ponds may be confined within ornamental walls rather than a gently sloping bank, and may have altered or reduced vegetation cover. The relative importance of pond size and connectedness versus local habitat features at a pond is therefore a key question for understanding the ecology of pond-breeding amphibians in cities, but also for identifying the best options for their conservation management.

Methods

Study area

Melbourne is Australia's second-largest city, supporting a population of approximately 4.5 million people. It has a temperate climate with a mean annual maximum temperature of 19.9 °C and a mean annual precipitation of 648 mm, distributed evenly throughout the year (Bureau of Meteorology 2017). Fourteen species of frogs inhabit the Greater Melbourne area, and ten of these are known to breed in lentic aquatic habitats such as ponds, lakes and dams (Anstis 2013).

Survey sites

I selected 104 sites at lentic water bodies (ponds) in public parks and gardens, from the center of the city to its rural fringe along an informal urban–rural gradient (Fig. 1). Sites were stratified according to pond size (two classes, < 200 and ≥ 200 m²) and the presence or absence of a vertical pond wall. See Parris (2006) for more information on site selection. Ponds ranged in size from 2 to 81,239 m², with a mean size of 467 m². The shortest distance between a pond and its nearest neighbor was 3 m and the longest was 12 km, with a mean of 514 m. I measured the area of small ponds in the field using a 25-m tape measure; larger ponds were measured using satellite imagery in ArcGIS.

The connectedness of a habitat patch can be measured in a variety of ways; I used the number of ponds within a 500-m radius of the target pond that were occupied by the species in question, excluding ponds that were isolated by a major road. This variable considers the number of other ponds supporting an extant population within dispersal distance of the target pond, rather than just the number or area of ponds within this distance. The latter two measures do not account for the habitat suitability of nearby ponds or their occupancy by the species in question, both of which are important considerations in metapopulation ecology (Heard et al. 2013). Only nearby ponds supporting extant populations can act as a source of immigrants to colonize the target pond following local extinction or to support a declining population (Hanski 1994b). There is little information on dispersal distances of the frog species in this study, but the smallest species (the common eastern froglet *Crinia signifera*) is known to disperse up to 500 m from ponds in a forested landscape (Lauck 2005). It is therefore likely that all four species can travel at least this distance if they are unhindered by substantial barriers in the urban landscape.

During habitat surveys at each site, I observed the presence or absence of a vertical pond wall, with a wall defined

Fig. 1 Map of Greater Melbourne showing the location of 104 ponds included in the study (*black circles*). Roads (*grey lines*) indicate the density of urban development across the region, while the Central Business District of the city is indicated by the *black triangle*

as a vertical drop from the pond bank to the surface of the water. Such walls are commonly constructed of stone, concrete or wood as an ornamental edging around ponds in urban parks and gardens (Parris 2006). I also measured the proportion of the pond area covered by emergent vegetation and submerged vegetation, plus the proportion of the pond edge that supported fringing vegetation other than short, mown grass. I then summed these values to give the total vegetation at a pond, with a maximum possible value of 3.

Frog surveys

I surveyed each site for frogs three times over two breeding seasons in spring–summer (September 2000–January 2001, and September–October 2001) using nocturnal searches. I recorded weather conditions during each survey, including dry- and wet-bulb temperature, wind speed, cloud cover and time since rain. Given the variable activity and thus detectability of frogs in the study area, three surveys were required to be confident of detecting the species present at a pond (Canessa et al. 2012). Nocturnal searches involved two people listening for the advertisement calls of male frogs at a site for 5 min, then searching the pond and surrounding banks and vegetation with spotlights and head

lamps for a minimum of 5 min. The time spent searching was proportional to the size of the pond, with 5 min of searching added for each 20 m of pond perimeter. When necessary for identification, frogs were caught by hand then released unharmed at the point of capture.

Data analysis

I assessed the influence of four explanatory variables on the probability of occurrence of each of the target frog species at a pond using Bayesian logistic regression with uninformative priors in OpenBUGS 3.2.3 (Lunn et al. 2009). These variables were log (pond size) in m² and pond connectedness (as proxies for metapopulation processes), plus the total vegetation at a pond and the presence or absence of a vertical pond wall (as indicators of species-environment or niche relationships). Pond vegetation provides important habitat for frogs, including shelter from weather and predators, calling sites for male frogs and attachment sites for egg masses. A vertical pond wall may limit use of a pond by ground-dwelling frogs that cannot climb vertical surfaces, as metamorphosing frogs cannot escape the water, become trapped in the pond and drown (Parris 2006).

I estimated the combined effect of the first two variables across their range of measured values when the second two were held constant at their mean (the metapopulation effect), and vice versa (the niche effect), to indicate whether metapopulation processes or local habitat features had the greatest influence on the probability of persistence of each frog species. I centered all explanatory variables (the centered value is the measured value of the variable minus its mean over all sites) to help reduce autocorrelation between successive samples obtained from the Monte Carlo Markov chain algorithm in OpenBUGS, and ran three chains for each model to check for convergence. For each chain, I generated 100,000

samples from the posterior distribution, thinned to one in every ten samples, after discarding the initial 150,000 samples as a burn-in. I calculated the mean and SD of the model coefficients, along with the 2.5th and 97.5th percentiles of the distribution which I used to represent a 95% credible interval (the Bayesian analogue of a 95% confidence interval). If working within the null hypothesis significance testing framework, a credible interval that does not encompass 0 would indicate that a null hypothesis of no effect could be rejected at $\alpha = 0.05$ (Cumming and Finch 2001).

Results

I detected nine species of frogs during the study, but only had sufficient records to model four of these: the common eastern froglet *C. signifera*, the striped marsh frog

Table 3 Coefficients (mean, SD, and 2.5th and 97.5th percentiles) of the explanatory variables included in the logistic regression model of the probability of occurrence of the striped marsh frog *Limnodynastes peronii*

Variable	Mean	SD	2.5%	97.5%
Intercept	− 1.508	0.3479	− 2.239	− 0.8763
Pond size	0.431	0.3237	− 0.1797	1.089
Pond connectedness	0.4324	0.1376	0.174	0.7138
Total vegetation	1.185	0.5666	0.109	2.334
Vertical wall	− 0.8875	0.8321	− 2.56	0.7193
Metapopulation effect	0.7566	0.1999	0.233	0.9789
Niche effect	0.4817	0.1536	0.1675	0.7589

The metapopulation effect is the combined effect of pond size and pond connectedness across their range of measured values when vegetation at a pond and the presence/absence of a vertical pond wall are held constant at their mean; the niche effect is the opposite

Table 2 Coefficients (mean, SD, and 2.5th and 97.5th percentiles) of the explanatory variables included in the logistic regression model of the probability of occurrence of the common eastern froglet *Crinia signifera*

Variable	Mean	SD	2.5%	97.5%
Intercept	− 0.01387	0.4995	− 1.009	0.9623
Pond size	1.193	0.4626	0.3622	2.178
Pond connectedness	0.5593	0.2121	0.2204	1.045
Total vegetation	0.8598	0.7022	− 0.4847	2.278
Metapopulation effect	0.9511	0.06455	0.7674	0.9989
Niche effect	0.693	0.1416	0.3786	0.916

Note that this species never occurred at a pond with a vertical wall. The metapopulation effect is the combined effect of pond size and pond connectedness across their range of measured values when vegetation at a pond is held constant at its mean; the niche effect is the opposite

Table 4 Coefficients (mean, SD, and 2.5th and 97.5th percentiles) of the explanatory variables included in the logistic regression model of the probability of occurrence of the spotted marsh frog *Limnodynastes tasmaniensis*

Variable	Mean	SD	2.5%	97.5%
Intercept	− 2.751	0.7998	− 4.485	− 1.356
Pond size	1.768	0.5826	0.7335	3.015
Pond connectedness	0.7229	0.2458	0.2758	1.243
Total vegetation	2.072	0.8112	0.5916	3.773
Metapopulation effect	0.9765	0.1612	0.8641	0.9997
Niche effect	0.3865	0.04108	0.1101	0.7175

Note that this species never occurred at a pond with a vertical wall. The metapopulation effect is the combined effect of pond size and pond connectedness across their range of measured values when vegetation at a pond is held constant at its mean; the niche effect is the opposite

Table 5 Coefficients (mean, SD, and 2.5th and 97.5th percentiles) of the explanatory variables included in the logistic regression model of the probability of occurrence of the southern brown tree frog *Litoria ewingii*

Variable	Mean	SD	2.5%	97.5%
Intercept	0.09157	0.2216	− 0.3436	0.5276
Pond size	0.7428	0.2458	0.2816	1.244
Pond connectedness	0.2845	0.09371	0.1078	0.475
Total vegetation	0.4877	0.4266	− 0.3441	1.334
Vertical wall	1.065	0.5974	− 0.07399	2.27
Metapopulation effect	0.8589	0.09394	0.6174	0.9725
Niche effect	0.4315	0.234	− 0.09225	0.8052

The metapopulation effect is the combined effect of pond size and pond connectedness across their range of measured values when vegetation at a pond and the presence/absence of a vertical pond wall are held constant at their mean; the niche effect is the opposite

Limnodynastes peronii, the spotted marsh frog *Limnodynastes tasmaniensis* and the southern brown tree frog *Litoria ewingii*, which were detected at 39, 30, 25 and 54 of the 104 sites, respectively. Pond area and connectedness (as measured by the number of ponds within a 500-m radius that were occupied by the species in question) were predicted to have a positive effect on the probability of occurrence of all four species of frogs (Tables 2, 3, 4, 5), although the credible interval for the effect of pond size on *L. peronii* encompassed zero, indicating some uncertainty about this relationship. Total vegetation at a pond also had a positive effect on the probability of occurrence of all four species (with some uncertainty for *C. signifera* and *L. ewingii*), but the presence of a vertical pond wall affected different species in different ways. *C. signifera* and *L. tasmaniensis* were never detected at a pond with a vertical wall. However, *Litoria ewingii*, a tree frog that can climb vertical surfaces, was more likely to be present at ponds with a vertical wall (Table 5), while *Limnodynastes peronii* showed the opposite trend (Table 3).

Metapopulation processes (as measured by pond size and connectedness) and niche or species-environment relationships (as measured by local habitat variables) had an important effect on the probability of occurrence of each species, but in all cases the effect of metapopulation processes was larger. For example, the difference in the probability of occurrence of *L. tasmaniensis* between the ponds with the best and worst metapopulation conditions (at a pond without a vertical wall, with total vegetation held constant at its mean)—the metapopulation effect—was 0.98, while the difference in the probability of occurrence between the ponds with the best and worst habitat conditions (with pond area and connectedness held constant at their mean)—the niche effect—was 0.39 (Table 4). In the case of *L. peronii*, the metapopulation and niche effects were more similar; the difference in the probability of occurrence between the

ponds with the best and worst metapopulation conditions (with total vegetation and presence of a vertical wall held constant at their mean) was 0.76, while the difference in the probability of occurrence between the ponds with the best and worst habitat conditions (with pond area and connectedness held constant at their mean) was 0.48 (Table 3).

Discussion

Results of this study indicate that pond size and connectedness had substantial positive effects on the probability of occurrence of all four species of frog. This provides support for the applicability of metapopulation theory in this study system; larger ponds are more likely to be occupied because of a lower probability of local extinction, while more connected ponds are likely to receive more immigrants to bolster an existing population or recolonize a habitat patch following a local extinction (Hanski 1994a). The cover of vegetation in and around a pond plus the presence or absence of a vertical wall also had important effects on the probability of occurrence of the four frog species. All species were more likely to occur at ponds with more vegetation. For adult frogs, vegetation in and around a pond provides important shelter from predators, calling sites for males of all species and attachment sites for the egg masses of *C. signifera* and *L. ewingii* (Anstis 2013). Submerged vegetation also provides tadpoles with shelter from introduced fish and other predators, mediating predation risk in urban ponds (Hamer and Parris 2013). The three ground-dwelling species (*C. signifera*, *L. tasmaniensis* and *L. peronii*) responded negatively to pond walls, to the extent that the first two of these were never detected at a walled pond. In contrast, the tree frog *L. ewingii*, an able climber, was more likely to be detected at ponds with vertical walls. These associations with local habitat characteristics indicate that niche or species-environment relationships are also important in this study system.

Insights from this study can be applied to the conservation management of urban amphibians in Melbourne and beyond. While substantially increasing the size of ponds may be impractical, measures to (1) increase connectivity between ponds (such as the construction of new, suitable ponds within 500 m of existing occupied ponds) and/or (2) reduce barriers to dispersal across the urban landscape could support the persistence of frog metapopulations. Increasing vegetation cover in and around ponds and/or removing vertical walls could also benefit some species. The contention that we must wait for a new theory of urban ecology to understand urban ecosystems may hinder practical conservation actions in cities. In contrast, recognizing the applicability of existing theory allows us to move quickly to design better urban environments for both biodiversity and people,

and to manage existing urban environments to improve their suitability for and utilization by frogs and other wildlife.

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