

Urban Ecosystems

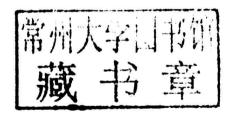
Ecological Principles for the Built Environment

FREDERICK R. ADLER

Department of Mathematics and Department of Biology, University of Utah

COLBY J. TANNER

Department of Ecology and Evolution, University of Lausanne





CAMBRIDGE UNIVERSITY PRESS Cambridge, New York, Melbourne, Madrid, Cape Town, Singapore, São Paulo, Delhi, Mexico City

Cambridge University Press The Edinburgh Building, Cambridge CB2 8RU, UK

Published in the United States of America by Cambridge University Press, New York

www.cambridge.org
Information on this title: www.cambridge.org/9780521769846

© Frederick R. Adler and Colby J. Tanner 2013

This publication is in copyright. Subject to statutory exception and to the provisions of relevant collective licensing agreements, no reproduction of any part may take place without the written permission of Cambridge University Press.

First published 2013

Printed and bound by CPI Group (UK) Ltd, Croydon CR0 4YY

A catalog record for this publication is available from the British Library

Library of Congress Cataloging-in-Publication Data

Adler, Frederick R.

Urban ecosystems : ecological principles for the built environment / Frederick R. Adler, Colby J. Tanner. pages cm

Includes bibliographical references and index.

ISBN 978-0-521-76984-6 (Hardback) - ISBN 978-0-521-74613-7 (Paperback)

 Urban ecology (Biology) I. Tanner, Colby J. II. Title 2. Urban ecology (Sociology). HT241.A35 2013
 307.76-dc23

2012040143

ISBN 978-0-521-76984-6 Hardback ISBN 978-0-521-74613-7 Paperback

Additional resources for this publication at www.cambridge.org/9780521769846

Cambridge University Press has no responsibility for the persistence or accuracy of URLs for external or third-party internet websites referred to in this publication, and does not guarantee that any content on such websites is, or will remain, accurate or appropriate.

Preface

This book describes the challenges and opportunities that urban environments present to the plants and animals that inhabit cities and the ways that those organisms and entire ecosystems respond. The broad outlines of life are always the same: the need to find resources, to avoid being eaten or being killed, and to reproduce successfully. Ecologists have long studied how these factors determine which species live in a particular place and how those species interact with each other and the ecosystem. Only recently, however, has the focus of ecological science turned to life in urban environments.

The science of ecology developed in the late nineteenth century through the integration of three advances: detailed natural history of species and their habits, Darwin's emphasis on species interactions and change over time, and improved understanding of the physiology of plants and animals. The new field struggled to define the very nature of its subject of study, the communities of plants and animals that coexist and interact in one place and time. Was each community a tightly knit whole or merely a loose assemblage? What key factors determine how communities function?

Faced by these fundamental questions, ecologists deferred thinking about the massive disruption that cities bring to natural processes until those processes themselves could be better understood. As that understanding emerged, ecologists began turning their attention to cities. The modern practice of urban ecology grew from several distinct sources. In nineteenth-century Europe, studies of the plants of urban gardens, cemeteries, and highly disturbed building sites established a foundation of natural history information. These studies were among the first to distinguish between introduced and native species, and show how urban climate and urban pollution determine which plant species persist.

Early studies in the United States focused on interactions between humans and nature. Contemporary with early studies on European plants, George Perkins Marsh emphasized the potentially catastrophic effects of humans on the environment. Faced by possible environmental collapse, the term urban ecology became linked with the ecological challenges underlying urban planning. A group of sociologists, often called the Chicago School, applied ecological ideas about communities, competition, and spatial spread to describe how humans and their institutions change over time. In her attack on traditional urban planning, Jane Jacobs stressed the ecological nature of cities, and the danger of ignoring how different elements interact.

The more purely ecological appreciation of urban plant and animal communities and the interplay between ecological thinking and social science have found a potential synthesis in the establishment of two long-term ecological research sites in the cities of Phoenix and Baltimore in the United States. The sites will be monitored for decades to provide baseline data on ecological functioning to parallel studies in non-urban forests, grasslands, and wetlands. In addition to providing fundamental ecological data, these studies have spurred the effort to create a new synthesis that links human and non-human elements into a single framework.

Organization of the book

This book is structured like a play, in five acts, each with several scenes.

- Act 1 introduces the setting, the built environment, and the protagonists, the nonhuman residents of the urban world.
- Act 2 introduces the basic tension between intended and unintended consequences.
- Act 3 is the rising action, with development of the abiotic factors such as nutrients and weather that create the challenges faced by the protagonists.
- Act 4 is the climax, where we find out which protagonists fare well, which fare badly, and why.
- Act 5 is the resolution that looks at humans as urban organisms and challenges us to think where we go from here.

For some characters, such as the rock pigeon, we could see this as a comedy. All ends well, and the pigeons celebrate a new order. For others, such as the wood thrush, it is a tragedy as their world disappears. For urban humans, it is neither a comedy nor a tragedy, but an epic backyard drama. Nothing is resolved, for the story continues and indeed accelerates, but we hope to emerge wiser and more observant, and better able to see the world and ourselves.

How to use this book

This book is based on a one-semester course at the University of Utah. It is designed either to be read directly or used in the classroom. In the classroom, rather than presenting information in lecture format over a single semester or quarter, we recommend mixing lectures with discussion and choosing to give some topics less detailed classroom coverage. Centering class discussion around short papers based on the articles highlighted at the end of each chapter gives students a chance to focus and share their own ideas. Coupling classroom activities with field trips, based on the availability of local experts and sites, shows that the ecology discussed in this book is everywhere. For example, streams and reservoirs illustrate the transformation of urban water movement, parks or brownfields illuminate the factors that control urban biodiversity and the distribution of invasive species, and the college campus itself provides an overview of urban land types and their management.

Intellectually, the central goal of this book is to provide a framework of fundamental principles for thinking about ecological processes in urban environments. For this reason, we present only statistically significant results, and do not include error bars that of course can be found in the primary references. But more immediately, we seek to make readers aware that urban ecosystems are indeed ecosystems, and that fundamental life processes are happening all around us. For most people, a city consists of buildings, roads, and the humans that use them, ignoring the ways that urban residents interact with ecology. Urban residents, often unwittingly, shape the ecology around them, while that ecology shapes the lives of urban humans, again whether or not they are aware of it.

While working on this book, we returned to Salt Lake City by plane, and looked out the window as the plane flew low over the Salt Lake Valley, over suburbs planted with trees that would not have been there 100 years ago, over the straightened and polluted Jordan River bordered by a thin and threatened strip of green, over warehouses with their abandoned areas overgrown with weeds, and over playing fields planted with nonnative grasses that can tolerate constant trampling, before descending into the paved expanse of the airport. These environments, so different from each other and so different from the sagebrush steppe on the surrounding foothills, were packed together in closely abutting contrast. How different this would be from the perspective of a bird or a floating plant seed! Filled though it is with charts and graphs very much of human origin, this book, we hope, is a path to seeing the urban world through different eyes.

Contents

	Preja	ce	page vii
1	Urban	ecosystems and the science of ecology	1
	1.1	Engineered ecosystems	2
	1.2	Urban habitats	4
	1.3	Urban organisms	16
	1.4	The science of ecology	23
	1.5	What makes urban ecosystems different?	30
	1.6	The goals of urban ecology	33
	1.7	Questions and readings	35
2	Urban	39	
	2.1	The urban metabolism	41
	2.2	Urban energy budgets	48
	2.3	The urban ecological footprint	55
	2.4	Comparison with other social organisms	62
	2.5	Questions and readings	68
3	Urban ecosystem processes		
	3.1	Urban climate	76
	3.2	The urban water cycle	91
	3.3	Urban nutrient dynamics	102
	3.4	Urban ecological amplification and its consequences	122
	3.5	Questions and readings	132
4	The ecology of urban organisms		
	4.1	Urban biodiversity	140
	4.2	Invasive species and biotic homogenization	161
	4.3	Species interactions in urban environments	175
	4.4	Urban infectious diseases	191
	4.5	Traits of urban organisms	202
	4.6	Urban evolution	231
	4.7	Questions and readings	240

j .	Impli	Implications of urban ecology			253
	5.1	Human health and disease			253
	5.2	Ecological principles and urban policy			265
	5.3	Cities and the future			281
	5.4	Questions and readings			284
	Glossary				291
	Refe	References Index of organisms			303
	Inde.				336
	Subj	Subject index			339

1 Urban ecosystems and the science of ecology

Every fall, the weather cools, the days shorten, the soil starts to dry, and leaves drop from deciduous trees in temperate regions. These leaves carpet the ground, changing how nutrients and water infiltrate the soil, determining which plants will grow the following spring, altering the insect community, and changing the very scent of the forest. How long these changes persist depends on the availability of water and warmth, and the properties of the leaves themselves, with some being highly resistant to decomposition and others far less so. Sometimes these changes are beneficial for the tree itself, and sometimes they are not. Trees do not drop their leaves in order to create these changes, but the changes come nonetheless, the final consequences of water moved from deep beneath the ground and sunlight captured and stored over the course of an entire summer.

A tree imports energy, water, and nutrients from a relatively small area around and beneath it to achieve ecological and evolutionary success through survival and reproduction. Weather conditions beyond its control force it to drop some of those hard-won imports, creating a whole set of unintended consequences for the tree itself as well as the surrounding ecosystem (Figure 1.1).

The central themes of this book reflect both the similarities and differences between cities and trees. Like a tree, urban areas change the habitats around them, and import and concentrate resources for a set of intended purposes. The concentration of these resources and the resulting outputs produce a panoply of unintended consequences. Compared with trees, however, urban areas draw a much wider array of resources from a much larger region, have a more pervasive effect on the environment they occupy, and export those effects over a broader area.

In this chapter, we lay out the groundwork for urban ecology. We begin by introducing the concept of the ecosystem engineer, a role played to perfection by urban humans. Next we meet some of the habitats in urban areas and the plants and animals that occupy them. This lays the foundation for reviewing the central questions of the science of ecology itself, how those questions fit within the urban context, and the major ways in which urban ecosystems differ from those with less human influence. Finally, we sketch the goals of the field of urban ecology, and of this book in particular.

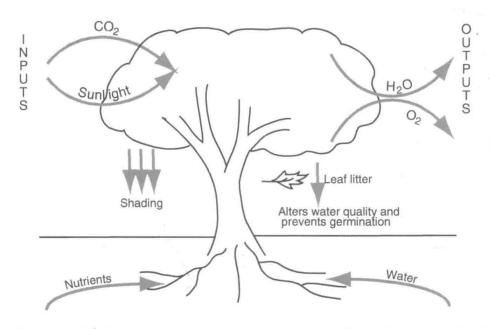


Figure 1.1 Like cities, trees import and export a whole range of materials, often transforming them in the process. These inputs and outputs create a wide array of intended and unintended consequences.

1.1 Engineered ecosystems

All organisms, however small, change their environment by their presence and by their use of resources. Most simply use available resources, with their existence affecting only a few nearby organisms. Early human hunter-gatherers may have shared the environment in this way, although early humans have been implicated in extinctions of some large mammals ¹⁸.

Other organisms, in contrast, have such major effects that they are termed *ecosystem* engineers ²⁸⁶ (Figure 1.2).

- Beavers build dams that change the flow of water, changing streams to ponds that flood surrounding forests.
- Woodpeckers drill holes in living or dead trees, making homes for themselves and other birds and animals, and opening up living trees to a range of pests and dead trees to decomposition.
- Trees change the climate and water flow patterns around themselves, and drop leaves that alter the properties of soil and determine which other plants can germinate and grow.
- Ants dig nests that alter the structure of soil and the movement of water within it, trim the vegetation around them, and import food and resources from many meters away. In this way, ants create "cities" with high densities of individuals that provide a revealing comparison with human cities.

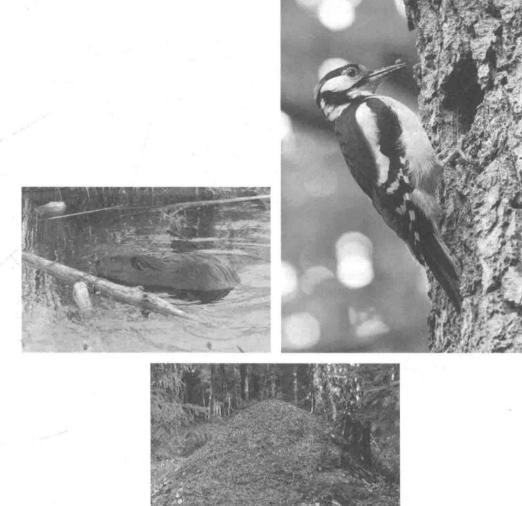


Figure 1.2 Three ecosystem engineers: beavers, woodpeckers, and ants.

These animals and plants transform the environment, shifting the balance from one type of community, such as a forest with few aquatic plants, to another, such as a pond with few trees. Low intensity agriculture falls into this category, where only a relatively small proportion of land is used for crop production and the intervening tracts continue to support relatively undisturbed flora and fauna.

Ecosystem transformation can take place to various degrees. Changes can be subtle, such as a hole in a tree, or they can be extreme, such as an entire ecosystem being replaced. A coral reef can turn a large area of shallow open ocean into a richly diverse community. A non-native plant, such as cheatgrass *Bromus tectorum* that now dominates vast stretches of western North America, can replace native flora and fauna with

a simplified and less diverse community. But it is modern humans who have mastered the art of ecosystem replacement.

Cities can change a shaded forest into a landscape of exposed rock, or a desert into a shaded forest. These transformed cities harbor an utterly different assemblage of plants and animals from the surrounding region, and have profoundly changed water movement and weather. The concentrated human demand for food requires large areas of high intensity agriculture, creating another set of novel environments that are dominated by single species such as corn, cattle, or soybeans.

Humans can be thought of as the definitive ecosystem engineers, making a whole range of changes simultaneously (damming rivers, building homes, moving resources, altering the climate) and over very large areas. But humans engineer the urban environment not just by modifying the locally available materials and resources, as beavers do by cutting and moving trees, but also by importing huge quantities of distant materials, energy, and nutrients, and exporting the resulting wastes. These unprecedented levels of input and output create, for the plants and animals that persist or flourish in the novel environment, an intensification of life similar to that experienced by the human residents of densely populated cities.

In some ways, however, humans have not so much created novel habitats as recreated or extended habitats favored by our distant ancestors ³⁴⁷. During human evolution, people left the forests for savannas and sought refuges in cliffs, caves, and rocky outcrops. Early cities, built with natural stone, recreate many of the rocky aspects of these habitats, although new structures of glass and steel do not. The other component of the ancestral human habitat, the savanna of mixed open country and trees, has been mirrored in the mix of lawns, gardens, and trees that make up the suburbs that many people prefer to inhabit ⁴¹⁹.

In urban areas, the effects of humans are never absent, almost by definition. Yet those effects vary in strength across the urban landscape, from preserved environments such as parks, transformed environments such as yards and gardens, to replaced environments such as buildings, roads, and landfills. How plants, animals, and other organisms make a living in this combination of environments is the central focus of this book.

1.2 Urban habitats

This book is about the functioning of ecosystems and the lives of plants and animals in the urban environment. But what, in fact, do we mean by "urban"? Many definitions are in use, often based on a specific population density threshold. For example, Japan defines urban areas by a density of at least 40 people per hectare. In comparison, the most densely populated city, Mumbai, India, has nearly 300 people per hectare, with the central zone packing over 1000 people into each hectare. This density exceeds that of a family of four living in a single-story 200 m³ square meter house by a factor of five, even without accounting for the yard, street, or other spaces between homes. The most densely populated US state is New Jersey, with just under five people per hectare. If the

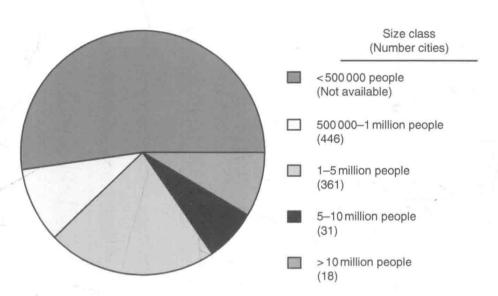


Figure 1.3 Percentage of urban people in cities of different sizes, along with the worldwide total number of such cities (after Gaston, 2010).

whole human population were spread evenly over the Earth's land area, there would be 0.5 people per hectare ⁶¹².

Other definitions involve the density of buildings or the distance between them ²⁰¹. This book is not tightly tied to any specific value, but focuses on how the changes characteristic of urbanization affect organismal and ecosystem processes. For planning purposes, different definitions can carry very distinct implications and must be considered more carefully ⁴⁶⁵.

By any definition, urban areas have grown vastly over the last three centuries. The first decade of the twenty-first century marks the first time in history when a majority of people live in cities, up from less than 10% in 1700²⁰¹. This leads to a concentration of the human population, with more than half the population in a small fraction of the Earth's habitable area. In fact, cities take up only 1–3% of the Earth's area (depending on the definition and the method of analysis) with agriculture and grazing taking up roughly 20% ⁵⁹⁵.

There are now over 400 cities with more than 1 million people, up from a handful before 1800, such as ancient Rome, medieval Baghdad, or industrializing London. The current urban population is distributed among cities of widely different sizes, with the majority in smaller cities and relatively few in the megacities of over 10 million people (Figure 1.3).

All ecosystem engineers modify habitats, and the urban environment includes some of the most modified habitats on Earth, the *built environment*. The urban environment, however, consists of a wide variety of habitats from completely built up to those with few or no buildings or roads. Urban habitats vary in their degree of modification, the type and amount of inputs, including pollutants such as excess nutrients or poisons such as arsenic. Although traditionally thought of decreasing from more to less built as a function of distance from an urban core, urban land use is in fact a complex and

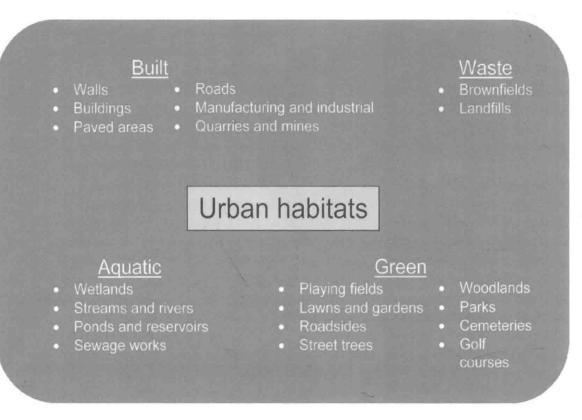


Figure 1.4 The various categories of urban habitat.

idiosyncratic response to historical and geological factors that rarely resembles a neat concentric arrangement 467.

We divide urban habitats into four broad categories (Figure 1.4).

- 1. Built habitats are structured primarily by human construction.
- 2. Waste habitats have been largely replaced with human discards.
- 3. Green habitats are covered primarily by plants.
- 4. Aquatic habitats are covered primarily by water.

Several careful inventories of urban lands show how different land uses are associated with different land types. In Manchester, UK, areas with high, medium, and low human population density differ in the percentage associated with different land cover ¹³⁴ (Figure 1.5). The built environment is broken into buildings and other *impermeable surfaces*, surfaces that water cannot penetrate, like roads and parking lots. With rare exceptions, even the most heavily populated areas have a substantial proportion of land covered with vegetation, with much of that taking the form of managed grasslands or lawns ³² (Figure 1.6).

Although all ecosystems include a range of habitat types, urban areas are unusual in having profoundly different habitats in close proximity with sharp transitions (Figure 1.7). From the perspective of organisms that can survive only in a few of these

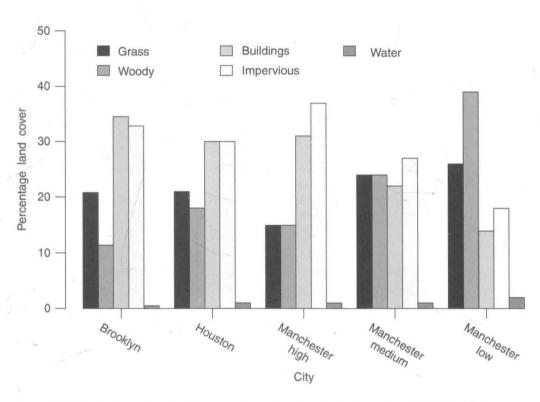


Figure 1.5 Distribution of habitats in two cities in the United States compared with in high, medium, and low density sections of Manchester, UK. High density areas have a preponderance of built habitats while low density areas are primarily green (after Douglas, 2011).

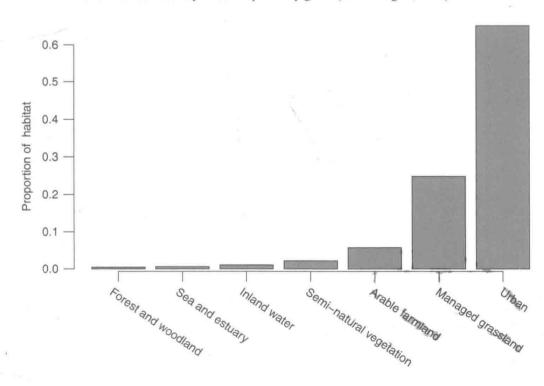


Figure 1.6 Distribution of habitats in London (after City Limits Report, 2002).

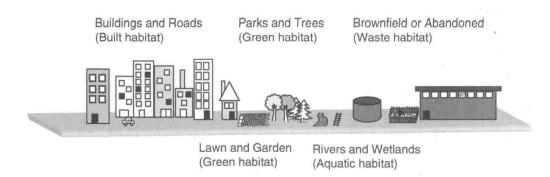


Figure 1.7 Urban areas contain a mix of contrasting and closely abutting habitats ranging from completely built by humans to nearly unmodified.

habitats, the urban environment can look like a set of habitat islands (often referred to as *patches*) separated by inhospitable environments.

Built habitats

Built habitats effectively define urban areas, designed for human use to the nearly complete exclusion of other organisms (Figure 1.8). Nonetheless, these habitats do support life, and the details of materials, architecture, and location determine which organisms can persist.

Walls in some cities cover as much vertical area as the city covers horizontally. Although generally quite inhospitable due to exposure to high levels of light, ultraviolet radiation, temperature and pollutants, and to low water availability, walls still accommodate some species. For example, walls built from porous materials such as limestone can support lichens, mosses, and climbing plants (Figure 1.9) along with a variety of algae and cyanobacteria ⁴⁸². Joints and cracks, particularly at the bottom of walls, provide places for water and nutrients to accumulate ⁶⁰⁷. The plants that survive in these islands of life can support communities of small insects, spiders, and snails ⁵⁷⁶.

Buildings include more complex physical structures than just their walls. Window gardens and roof gardens support small communities of flowers and plants (Figure 1.10). The physical structures of buildings provide nesting sites for birds of prey such as falcons that feed on the pigeons and sparrows that inhabit the city center, roof-nesting birds such as gulls, shorebirds, and ravens, and bats and swifts that nest in chimneys and attics. Within buildings, humans share space with a variety of "pests", such as mice, rats, and roaches, in addition to overwintering insects like moths and beetles. Spiders capture insects that enter either accidentally or intentionally to find food, water, or trash.

Paved areas include sidewalks, parking lots, and city squares. Plants that colonize paved areas must overcome the challenges of trampling and compacted soil, but those that succeed can flourish in pavement gaps that accumulate water and nutrients. In the most trampled areas, only low-growing herbaceous plants and grasses tend



Figure 1.8 The built environment of Paris.



Figure 1.9 Aging building walls can provide habitat for hardy plants.