Review

CellPress

Evolution of the indoor biome

NESCent Working Group on the Evolutionary Biology of the Built Environment, Laura J. Martin[1], Rachel I. Adams[2], Ashley Bateman[3], Holly M. Bik[4], John Hawks[5], Sarah M. Hird[4], David Hughes[6], Steven W. Kembel[7], Kerry Kinney[8], Sergios-Orestis Kolokotronis[9], Gabriel Levy[10], Craig McClain[11], James F. Meadow[12], Raul F. Medina[13], Gwynne Mhuireach[14], Corrie S. Moreau[15], Jason Munshi-South[9,16], Lauren M. Nichols[17], Clare Palmer[18], Laura Popova[19], Coby Schal[17,20], Martin Täubel[21], Michelle Trautwein[22], Juan A. Ugalde[23], and Robert R. Dunn[17,24]

[1] Department of Natural Resources, Cornell University, Ithaca, NY 14853, USA
[2] Department of Plant and Microbial Biology, University of California Berkeley, Berkeley, CA 94720, USA
[3] Department of Biology, Institute of Ecology and Evolution, University of Oregon, Eugene, OR 97403, USA
[4] UC Davis Genome Center, University of California Davis, Davis, CA 95616, USA
[5] Department of Anthropology, University of Wisconsin–Madison, Madison, WI 53706, USA
[6] Department of Entomology, Penn State University, University Park, PA 16802, USA
[7] Département des Sciences Biologiques, Université du Québec à Montréal, Montréal, QC H3C 3P8, Canada
[8] Department of Civil, Architectural, and Environmental Engineering, University of Texas at Austin, Austin, TX 78712, USA
[9] Department of Biological Sciences, Fordham University, Bronx, NY 10458, USA
[10] Department of Philosophy and Religious Studies, Norwegian University of Science and Technology, NO-7491 Trondheim, Norway
[11] National Evolutionary Synthesis Center, Durham, NC, 27705, USA
[12] Biology and the Built Environment Center, Institute of Ecology and Evolution, University of Oregon, Eugene, OR 97403, USA
[13] Department of Entomology, Texas A&M University, College Station, TX 77843, USA
[14] Department of Architecture, University of Oregon, Eugene, OR 97403, USA
[15] Department of Science and Education, Field Museum of Natural History, Chicago, IL 60605, USA
[16] Louis Calder Center–Biological Field Station, Fordham University, Armonk, NY 10504, USA
[17] Department of Biological Sciences, North Carolina State University, Raleigh, NC 27695, USA
[18] Department of Philosophy, Texas A&M University, College Station, TX 77843, USA
[19] Barrett Honors College, Arizona State University, Tempe, AZ 85287, USA
[20] Department of Entomology, North Carolina State University, Raleigh, NC 27695, USA
[21] National Institute for Health and Welfare, Department of Health Protection, 70210 Kuopio, Finland
[22] California Academy of Sciences, San Francisco, CA 94118, USA
[23] Centro de Genómica y Bioinformática, Facultad de Ciencias, Universidad Mayor, Santiago, Chile
[24] Center for Macroecology, Evolution and Climate, Natural History Museum of Denmark, University of Copenhagen, Universitetsparken 15, DK-2100 Copenhagen Ø, Denmark

Few biologists have studied the evolutionary processes at work in indoor environments. Yet indoor environments comprise approximately 0.5% of ice-free land area – an area as large as the subtropical coniferous forest biome. Here we review the emerging subfield of 'indoor biome' studies. After defining the indoor biome and tracing its deep history, we discuss some of its evolutionary dimensions. We restrict our examples to the species found in human houses – a subset of the environments constituting the indoor biome – and offer preliminary hypotheses to advance the study of indoor evolution. Studies of the indoor biome are situated at the intersection of evolutionary ecology, anthropology, architecture, and human ecology and are well suited for citizen science projects, public outreach, and large-scale international collaborations.

Corresponding author: Martin, L.J. (LJM222@cornell.edu).
Keywords: urban ecology; anthrome; microbiome; phylogeography; built environment.

0169-5347/
 http://dx.doi.org/10.1016/j.tree.2015.02.001

Glossary

Biome: Robert H. Whittaker first developed the biome concept to classify the different realms of life found on Earth. His classification scheme was based on two abiotic factors – precipitation and temperature – that he viewed to have the largest impact on the distribution of species and their traits and function. Subsequent biome classification systems have considered the biomes found in the absence of human agency and so exclude much of Earth's terrestrial area. One exception is the anthrome framework, which includes biomes engendered by humans [2]. However, even anthromes deal only with outdoor environments.
Indoor biome: the ecological realm comprising species that reside and can (although do not necessarily always) reproduce in enclosed and semi-enclosed built structures.
Indoor environment: the space enclosed by walled and roofed structures built by organisms to shelter themselves, their symbiotic partners, or stored goods. For the purposes of this review we focus on the indoor environments created by humans.

The indoor biome

Evolution occurs everywhere, even in the most densely settled places. Indeed, Darwin based his arguments for natural selection on domesticated plants and animals. Recent work in the fields of evolutionary biology, ecology, anthropology, and building sciences turns our attention back to species that coexist with humans. Much of this work is conducted in outdoor spaces [1], but a growing body of work addresses evolution in the indoor biome (see Glossary).

The indoor biome is expansive. Estimates of the extent of residential and commercial buildings range between 1.3% [3] and 6% [4] of global ice-free land area, an area as extensive as other small biomes such as flooded grasslands and tropical coniferous forests (Figure 1). In addition, whereas the area of flooded grasslands and tropical coniferous forests is shrinking, that of the indoor biome is rapidly growing [5], as is our ability to study indoor species thanks to citizen science, new approaches in genetics, and calls to integrate humans into the ecosystem concept [6–10] (Figure 2).

Here we review the rich but fragmented literature on evolution in the indoor biome. For the purpose of brevity we restrict our examples to one type of built structure – human dwellings – although the indoor biome encompasses all built structures (Box 1, Table 1).

Box 1. Built structures other than houses

In this review we have focused on houses, but many other buildings constitute the indoor biome. These include places of worship, food storage areas, commercial spaces, factories, offices, and restaurants [2]. In addition, houses are not closed systems; many materials flow into and out of them. For instance, a diverse range of microorganisms is present in municipal water supply and piping biofilms that enter homes via water lines, so mapping the inflow and outflow of organisms into the indoor biome may be a nontrivial challenge. Furthermore, it should be recognized that studies of indoor biomes cannot avoid intersecting questions of politics and justice. It should not be taken for granted that humans live in houses. An estimated 100 million people were homeless in 2005 [United Nations Commission on Human Rights (2005) Press briefing by special rapporteur on right to adequate housing (http://www.un.org/News/briefings/docs/2005/kotharibrf050511.doc.htm)], while human structures are sometimes abandoned and may persist as indoor environments without a human presence. It should also not escape notice that structures also vary widely by place. For example, approximately 50% of Canadians live in houses with seven or more rooms, while only 9% of people from Burkina-Faso do so [United Nations Department of Economic and Social Affairs (2012) Table 21. In *Compendium of Housing Statistics* (http://unstats.un.org/unsd/demographic/sconcerns/)]. It is therefore important, as with all biological studies, to be context specific [75].

A brief history of the indoor biome

The nests of birds, termites, and ants are part of the extended phenotype of those organisms, as are those of our closest living relatives, the great apes, which construct nests across a broad range of environments. Our common ancestors would probably also have used regular sleeping places with constructed nests [11]. Primate nests, like modern built environments, are places where bodies habitually rest and thus suitable places for organisms that depend on access to bodies to reproduce. How the nest is constructed thus influences the species to which the builder is exposed. Chimpanzees choose nesting sites and construction methods that reduce arthropod parasites [12], suggesting that, in the past, parasites imposed selection on primate nesting behavior. Meanwhile, the evolutionary history of many human ectoparasites and commensals, including body lice, *Demodex* mites, and bacterial symbionts, predates the origin of apes (and hence almost

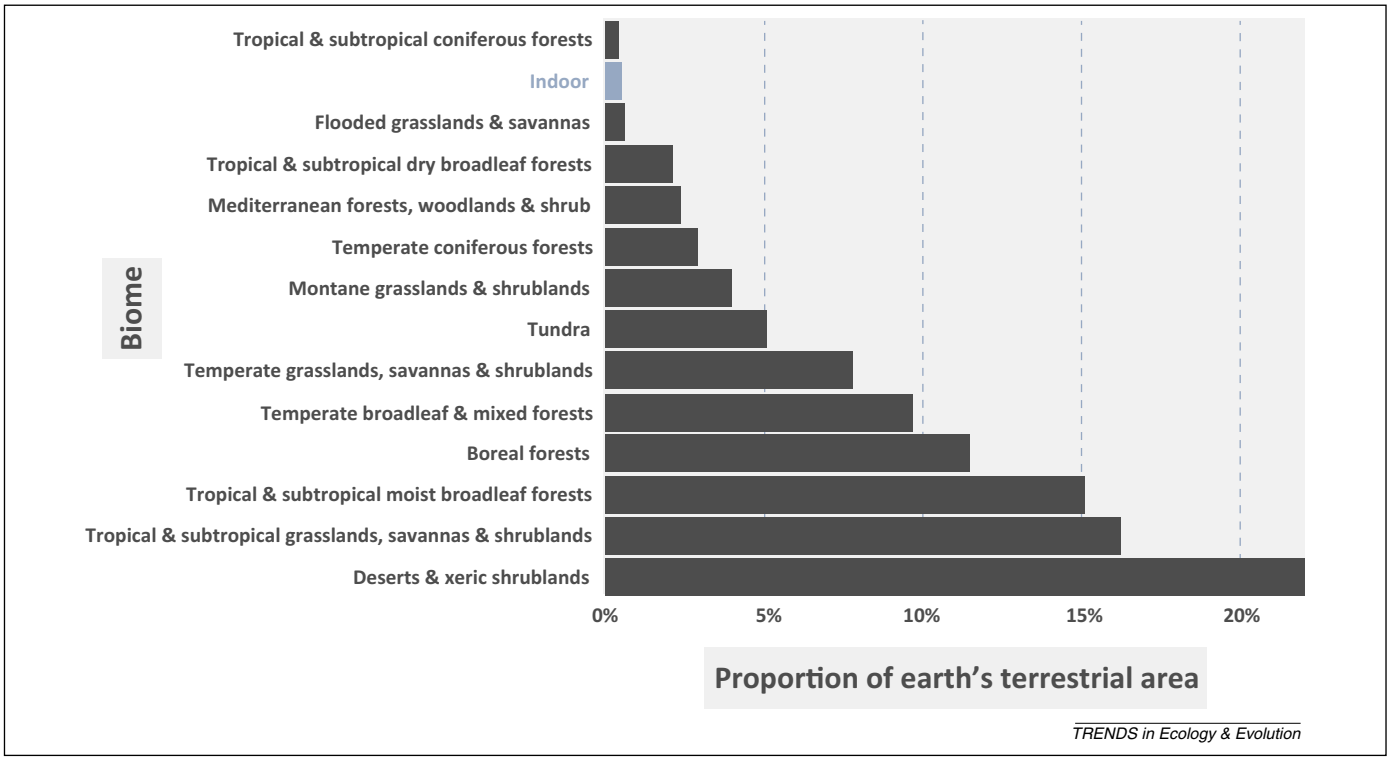

Figure 1. The relative areas of 13 outdoor biomes and the indoor biome.