

Evolution of the indoor biome

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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.

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.

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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](#)).

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

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].

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

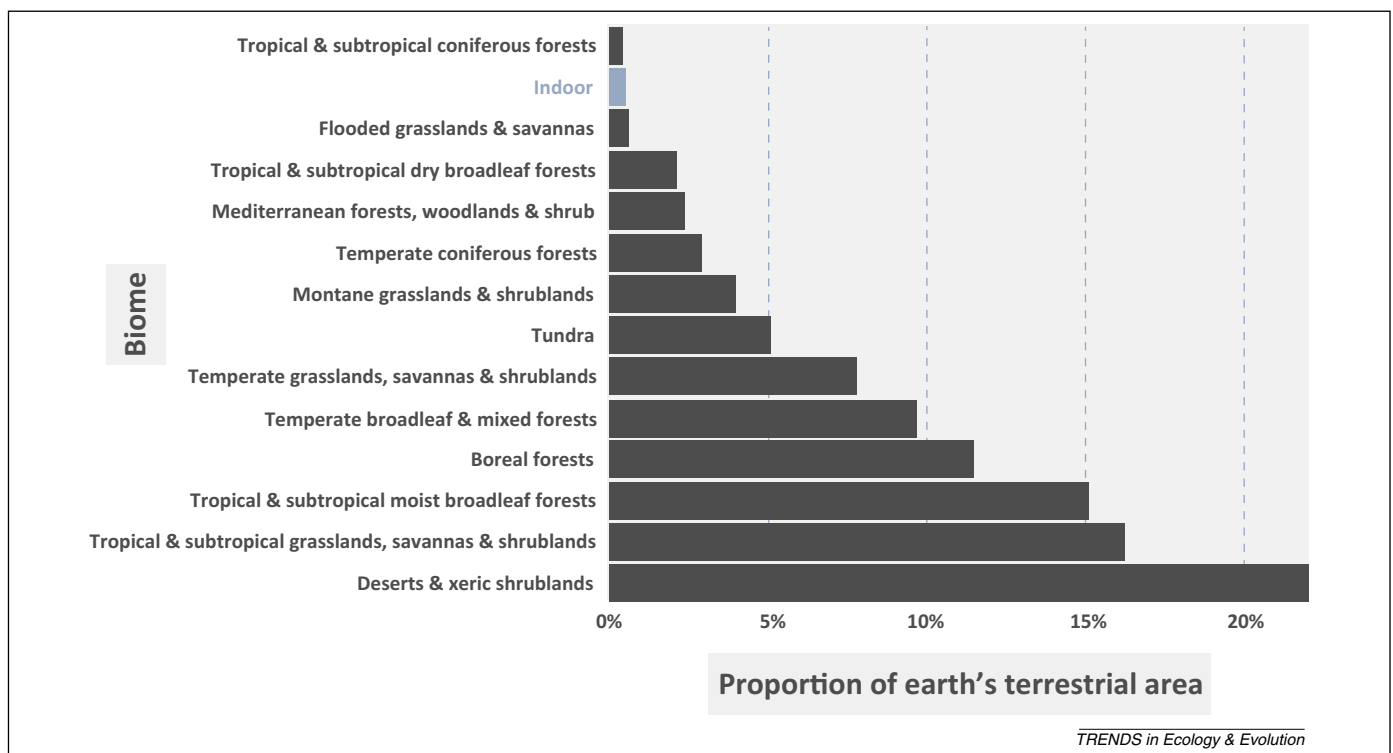


Figure 1. The relative areas of 13 outdoor biomes and the indoor biome.

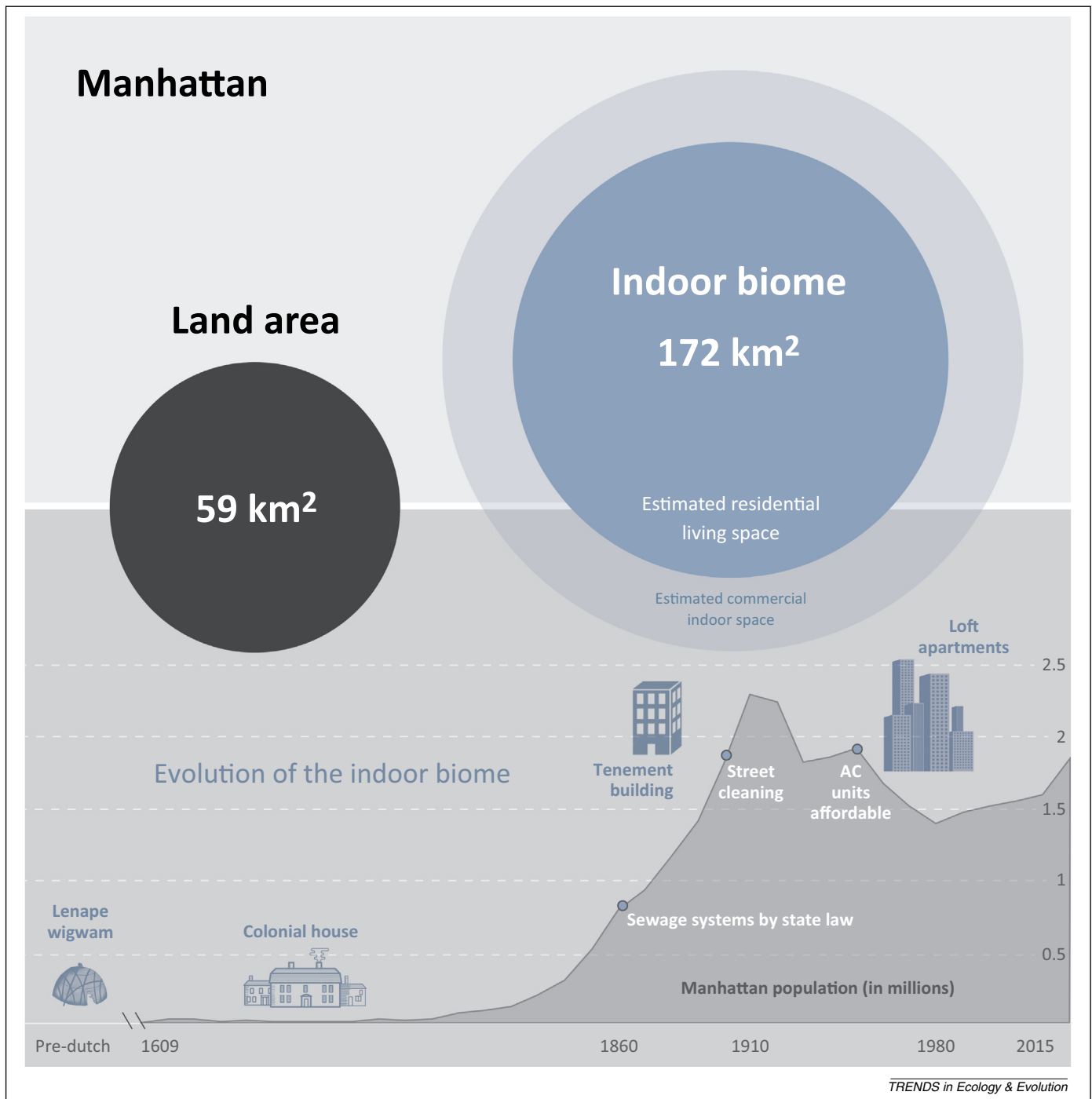


Figure 2. The trajectory of the indoor biome in one exemplar area, the island of Manhattan. The indoor biome in Manhattan is now nearly three times as large, in terms of its floor space, as is the geographical area of the island itself. Historically Manhattan was an outlier, but as urban populations grow much, perhaps most, of the world's population will soon be living in areas with more floor space than dirt. Included on this figure are key changes in the development of the indoor biome, as manifested in Manhattan. These changes are neither universal in the indoor biome nor necessarily unidirectional (the population, for instance, in Manhattan declined in the early 1900s), yet, as emphasized in the text, when they occur have the potential to have large but poorly studied consequences on evolution indoors.

certainly the first ape nest) [13,14]. Other species that inhabit contemporary houses, including dust mites, some beetles, and webbing clothes moths – many of which are found in contemporary nests of mammals or birds – may have first become associated with our ancestors subsequent to their construction of nests (e.g., [15]).

With time, some primates began to use caves as sleeping sites [16]. Caves share more similarities with human houses than do nests, as they are less variable in terms of climate than the outdoor environment and represent

places where ectoparasites and other associates of hominids could reliably find bodies and food. Bed bugs (*Cimex lectularius*), for example, are speculated to have moved from bats onto humans during a time when humans occupied cave environments [17].

The first human houses emerged approximately 20 000 years ago [18]. Before the origin of agriculture, houses were places where humans slept, mated, and ate and where refuse accumulated. After the origin of agriculture, trajectories differed among regions. In some regions,

people shifted from sedentary to nomadic lifestyles or from high- to low-density settlements [19]. Eventually, however, in virtually all inhabited regions, urbanism arose, and with it higher-density living.

Initially, humans designed houses to take into account the climatic conditions of specific places [20]. Increasingly, however, technological and political developments have changed the relationship between house design and the outdoor environment in affluent countries, cities, and neighborhoods. As a result, apartments in Finland and Singapore may now be very similar, independent of their very different settings. These developments include: the adoption of indoor plumbing in the late 1800s; electrification and air conditioning of residences in the 1920s; electrification of farms in the USA in the 1930s; and new standards for ventilation and insulation following energy crises in the 1970s (Figure 3).

Nevertheless, modern analogs of many historic indoor biomes still exist (and in some regions predominate). As a result, the global diversity of conditions within the indoor biome is likely to be as great as it has ever been. For the purposes of this review we attempt to consider the evolution of the indoor biome in light of the great modern and historical variation in homes, but note that most studies of indoor evolution are done in relatively new, relatively large houses in North America and Europe.

Species of the indoor biome

Thousands of species – perhaps hundreds of thousands – live in the indoor biome, many of them preferentially or even obligately. A study of just nine habitats (e.g., kitchen, bedroom) in each of 40 houses in North Carolina, USA, documented more than 8000 bacterial and archaeal taxa through molecular detection [21], while a study of 50 houses in North Carolina, USA noted more than 750 arthropod species, with often more than 100 species of arthropod per house (M. Trautwein, unpublished). Similarly, a molecular-based survey of 11 houses in California, USA, found hundreds of fungal taxa [22], and dozens of fungal species have been cultured from showers and drains alone [23]. Strong biogeographical patterns have been identified for bacteria in residential kitchens [24] and inhabitants in a new home can drastically influence the home microbiome within a matter of days [25]. Molecular surveys have also identified a suite of microscopic species in treated drinking water [26].

What we know today about the natural history of the indoor biome derives from the relatively small proportion of indoor species that have been studied in any detail (Box 2), a group biased toward species that humans attempt to exclude from the indoor biome. It is from these species that we begin to derive a more general story of the evolution of the indoor biome.

Selection pressures in the indoor biome

Perhaps the only intentional actions humans take to alter evolution in the indoor biome are attempts to extinguish disliked species, whether through cleaning practices, the use of biocides, or attempts to prevent species from colonizing in the first place. The organisms subject to biocide differ across regions and cultures as a function of which

animals are feared or disliked. What does not seem to vary is a dislike or fear of at least a few organisms that live in the home [27]. In many instances, the use of biocides has led to the local extinction of susceptible genotypes and the increase of less susceptible ones. Many insect species have evolved resistance to insecticides [28], for example, and multiple rodent species have evolved resistance to rodenticides [29]. Such species have evolved both the ability to tolerate biocides and the behavior of avoiding biocide ingestion. German cockroaches (*Blattella germanica*) have evolved an adaptive behavioral aversion to glucose in poison baits [30]. Many bacteria have evolved resistance in response to the use of antibiotics in living facilities and hospitals (e.g., [31]) and in the production of domestic food animals (e.g., [32]). The antimicrobial triclosan has been suggested to disfavor some microbial lineages in sink drains while, like most biocides, favoring others [33].

Other selective pressures in houses remain unstudied. These selective pressures result from choices humans make as a result of their preference for living conditions, design, or indoor climate. Globally, the distribution of indoor climatic conditions and resources varies widely because of both variation in outdoor climate and differences in the extent to which different types of home buffer that climate. Many of the Western houses that have been the focus of studies on indoor taxa are relatively decoupled in terms of their climate from outdoor conditions (e.g., Figure 3A), such that many species of the indoor biome are likely to have experienced recent selection favoring lineages able to tolerate dry, warm habitats (Figure 3A,B) relative to those that prefer moist, cool habitats [34]. While seasonal patterns in temperature and humidity are buffered by houses, the extremes at smaller scales (centimeters and minutes rather than kilometers and days) can be as great as those outdoors. Even within a single house, temperature, humidity, salinity, pH, and other environmental variables can span nearly the full range observed globally outside. Bathroom showerheads, for instance, can go from completely dry to saturated within hours (which favors microorganisms able to take advantage of moisture-pulse events, including pathogens) [23].

In the following sections, we outline three questions for future research. (i) How did species come to populate the indoor biome? (ii) Which traits does the indoor biome select for? (iii) How will changes in human culture affect indoor evolution?

On the origin of indoor species

Little research explores how species come to populate the indoor biome. We hypothesize that, in many cases, preadaptations allow species to colonize built structures and then, having colonized, these species respond to local selection pressures. The grain weevil (*Sitophilus granarius*) appears to have evolved to feed on grains stored by ants and rodents and thus was preadapted to make the transition to grains stored by humans [35]. However, since colonizing human-stored grains, *S. granarius* is likely to have experienced strong selection for traits that facilitate survival in the very different conditions of granaries. Similarly, rodents of the genus *Rattus* appear to have been predisposed to success as human commensals, with 14 of

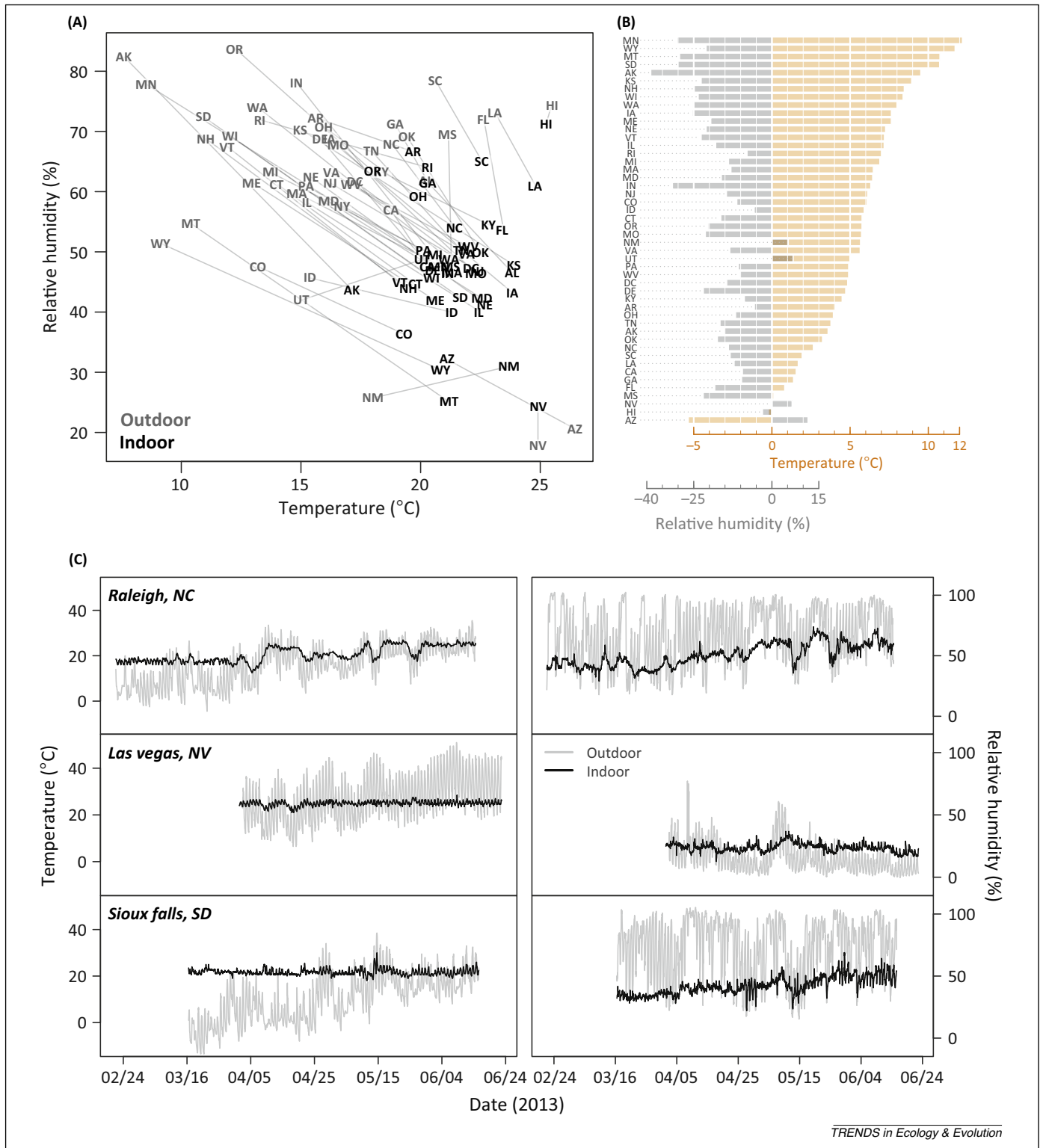


Figure 3. Ambient conditions in the indoor biome can differ substantially from outdoor conditions. **(A)** Paired outdoor (light gray) and indoor (black) values of mean relative humidity and mean temperature recorded in 47 US states and the District of Columbia across a 4-month period. During this part of the year, most houses tend to be warmer and less humid than adjacent outdoor environments, but some states, particularly in the southwest USA, do not follow this trend. **(B)** Localities within the USA differ in their relative differences between indoor and outdoor ambient conditions. Orange bars show the difference between mean indoor and outdoor temperatures. Gray bars show the same difference for relative humidity. **(C)** Three examples from across the USA demonstrate the difference in temporal variability depending on locality. Hourly point temperature (°C) and percentage relative humidity measurements outdoors (gray) and indoors (black) across three states. Data recorded by iButton[®] data loggers (Hydrochron iButton model DS1923; Maxim/Dallas Semiconductor, Dallas, TX) between February 24, 2013 and June 24, 2013.

Box 2. Categorizing species of the indoor biome

The species of the indoor biome can be separated into 'intended introductions' and 'unintended introductions'.

Intended introductions are species that humans intentionally bring into indoor environments, often supporting their metabolism and sometimes reproduction. These species include pets, houseplants, and species used for food fermentation. Such species possess traits that increase their probability of being indoors; these traits and species evolve as humans select some lineages over others, either intentionally or otherwise. While some intended introductions may be true mutualists of humans, the fitness advantage of living with humans for some other organisms, such as domestic cats or flowering plants, is less clear (but see [76]).

Unintended introductions constitute the other species found in the indoor biome – species that have long been associated with humans but have been ignored by humans or deterred from occupying human dwellings. These species include human commensals, pathogens, and parasites as well as mammals, arthropods, fungi, and other species that use indoor environments opportunistically. Many of these species, such as rats (*Rattus* spp.) and the house mouse (*Mus musculus*), have ancient relationships with humans and have spread with humans and particular human cultures.

The above framework excludes species that passively drift into houses from surrounding environments but are not metabolically or reproductively active inside houses. For these species, houses are essentially restaurants, hotels, or cemeteries (ecological sinks or traps). 'Peridomestic' species, for example, feed indoors and reproduce outdoors [77].

61 species found inside the indoor biome in at least some region [36]. We speculate that fungal and bacterial species in the home may also include taxa that were preadapted for colonization, but in most cases too little is known about indoor microbes to identify their colonization history. For example, Abe and Hamada found that *Scolecobasidium* fungus isolated from bathrooms and washing machines formed a distinct clade most closely related to *Scolecobasidium humicola* isolated from plant litter [37]. It is possible that fungal isolates from bathrooms represent a recently evolved lineage adapted to indoor, soapy environments ([38] suggested as much). However, it is also possible that the lineage from which these indoor populations derive has simply not yet been sampled. As another example, the bacterium *Thermus aquaticus*, which is often found in water heaters, was originally hypothesized to have evolved from ancestors from hot springs [39] but no one has yet studied how this colonization event might have occurred.

Phylogeographical and phylogenomic advances promise to elucidate the stories of both indoor species and the humans with whom they have traveled. Studies of the black rat (*Rattus rattus*) reveal a complex history in which rats colonized human built environments multiple times independently in different regions [40]. The subsequent history of evolution in these lineages illuminates patterns of human migration and trade. The phylogeography of insular populations of black rats reveals that many distinct lineages have evolved since the human colonization of Indian Ocean islands and these lineages reflect the individual colonization histories of different islands [41,42]. The spread of the Norway rat (*Rattus norvegicus*) was later than that of the black rat (although also out of Asia) and as it spread the Norway rat displaced the black

rat in many regions [43], setting the stage for the possibility of evolution in both species in response not only to climatic gradients and isolation but also to each other's presence. Given that *R. rattus* has colonized most of the world and, in doing so, now experiences great variation in human living conditions, the species represents a potential model organism for the indoor biome.

Most indoor taxa, despite being encountered every day, have evolutionary histories that are poorly resolved. The case of roaches is emblematic of the huge gaps that exist even for species that are considered well studied. For decades, it has been known that the center of species diversity of the cockroach genus *Blattella* is Southeast Asia, but only one of the 51 species, the German cockroach (*B. germanica*), has become so specialized in the built environment that it is not known to occur anywhere else [44]. Although several studies have considered local population dynamics in *B. germanica*, none has considered its evolution relative to its likely sister taxa or wild populations in the region in which it is putatively native. The situation is similar for most indoor species, be they animals, plants, fungi, bacteria, or others.

Our knowledge of the indoor biome would benefit from phylogeographical and phylogenomic comparisons that include both indoor taxa and outdoor congeners (e.g., [46]). The common bed bug (*C. lectularius*), for example, occurs only in the built environment and has congeners in nature – bat bugs – that could inform us about evolution in the indoor biome [45]. The challenge in many cases will be identifying potential sister lineages to include in analyses. *Exophiala*, for example, is a black yeast commonly found in sinks and dishwashers in houses and on steam-bath walls. Its known counterparts in outdoor areas are found on the skins of tropical fruits and, because of its occurrence patterns, thermotolerance, acid tolerance, osmotolerance, and melanization, its natural life cycle is thought to be tied to that of frugivorous animals in the tropical rain forest [47]. However, closer relatives might live in other habitats but have not yet been studied.

Which traits does the indoor biome select for?

Many household organisms share phenotypes and behaviors with cave-dwelling organisms. Many indoor arthropods have flattened bodies (e.g., bed bugs, cockroaches, silverfish), presumably because this body type better fits in crevices within houses. Some arthropods in houses, like those that live in caves, have less acute vision but longer antennae, which are often used to orient to edges (e.g., cockroaches, silverfish, crickets). Cave-dwelling microbes are relatively unstudied but, based on the similarity of food sources, substrates, and climates in caves and homes, some species of house-dwelling microbes may have evolved in caves.

In caves, animals tend either to lose their ability to disperse (because dispersal is costly and the odds of finding a new cave are low) or to evolve the ability to disperse passively with animals able to travel to new caves, such as bats. We predict a similar pattern in the indoor biome, particularly in regions in which indoor and outdoor conditions are very different. Urban populations of the weed *Crepis sancta* that inhabit tree pits surrounded by concrete

have adapted to produce non-dispersing seed types at a higher frequency than rural populations [48] because it is better to stay in a crowded pit than to die on the cement. Wingless and blind invertebrates are common in barns, where stored products are predictably transported, and are patchily distributed at geographical scales that are large relative to the ability of most invertebrates to actively disperse [49]. Similarly, many indoor species appear to have reduced dispersal ability. Camel crickets, some roach species, bed bugs, silverfish, and booklice lack flight, although flightlessness is relatively rare among insects [50,51]. Even winged animals found indoors, such as webbing clothes moths, are often poor flyers [15].

Many bacteria in homes and human-dominated environments appear to be sufficiently ubiquitous in the air that they are neither dispersal limited [52] nor able to prevent dispersal into bad habitats. For these taxa, selection may favor tolerance of indoor conditions (and their fluctuation) rather than particular dispersal traits. Other taxa of bacteria and other microbes are able to reliably enter houses on humans and their pets [21,25] or arthropods [53] and some food-borne taxa arrive in houses within food.

In all organisms in homes, except those able to easily move in and out, the fluctuating conditions experienced at small scales in homes, such as on showerheads, should favor tolerance of fluctuating stresses [23]. For arthropods, this often involves reduction in metabolic activity. Indoor ectoparasites (e.g., fleas, bed bugs) have evolved metabolic strategies to withstand long periods without their human or pet host (e.g., lower metabolic rate, delayed molting, ability to engorge to several times their body mass) [54]. Indoor silverfish (*Lepisma saccharina*) and firebrats (*Thermobia domestica*) can survive long periods of starvation and firebrats can actively absorb water from the atmosphere [55]. Meanwhile, one of the most common fungi in houses, *Aspergillus fumigatus*, can grow across a broader range of temperature conditions than other related taxa – an ability that may facilitate its survival in varied indoor habitats [56]. Additionally, the bacterium *Deinococcus radiodurans*, known for its extreme desiccation and UV tolerance, appears to accumulate in building dust over time indoors [57]. The adaptations that allow microbes to survive in episodically stressful conditions, such as those present in dishwashers, showers, and sinks, may also favor pathogenic species and perhaps even the evolution of pathogenicity [58] – a worrisome hypothesis, given that we have recreated these conditions in houses across the world.

Interestingly, the dependence of many indoor species on passive or facilitated dispersal means that the composition of species in a particular built structure is likely to be stochastic (with the stochasticity being greater where the amount of movement into the home is lower and for taxa with poorer dispersal abilities). Both roaches and bed bugs in apartments seem often to derive from single introduction events [59]. Until relatively recently, Norway rats were unable to colonize Phoenix, AZ due to the relatively inhospitable climate around the city [36]. As a consequence of the stochasticity of colonization, parthenogenetic reproduction may be favored indoors. At least some species that thrive indoors are facultatively parthenogenetic [e.g., the

American cockroach (*Periplaneta americana*), the Surinam cockroach (*Pycnoscelus surinamensis*)] [60]. Whether the incidence of parthenogenesis in indoor species is unusually high has not been formally tested. *A priori*, animal species that reproduce indoors may also have evolved the ability to tolerate extensive inbreeding. Whether particular reproductive strategies might also be favored in microbes in indoor environments does not appear to have been considered.

How will changes in human culture affect indoor evolution?

Subtle features of human culture have the potential to have large impacts on evolution indoors. The spread of parasites and other infectious agents often depends on intimacy among humans and between humans and other animals. For example, genital lice (*Phthirus pubis*) moved from the ancestor of gorillas to humans in a moment of some form of intimacy [61]. Close interaction has allowed new microbes to enter human habitats through meat, milk, dung, and common vectors (like flies, fleas, and ticks). Classic epidemic viral diseases of humans have their origins in the animals that were domesticated early [62,63]. In some cases, intimate interactions with nonhuman animals lead to the colonization of humans and homes with species that spread globally; in others, they seem likely to lead to more local populations.

A related aspect of human culture that may affect the evolutionary trajectories of indoor species is a preoccupation with purity and pollution [64]. Many of the visible organisms found in houses have a ‘disgust-evoking status’. However, the organisms that elicit these responses vary from place to place (although see [27]), as do the social stigmas related to these organisms. Cultural conceptions of what is clean or dirty ultimately drive how we behave toward indoor species, especially those that we label ‘pest species’, and consequently how we shape the indoor biome [65]. One could argue, for example, that the widespread presence of antibiotic resistance in the USA is due to an industry-driven response to a cultural construct: the idea of ‘germs’ [66]. The study of the influence of culture on indoor evolution offers rich potential for new discoveries and important case examples of rapid evolution.

Ecological theory suggests that the spatial arrangement and density of indoor spaces within a region may also have an impact on the evolution of indoor species, particularly for those whose fitness is higher indoors than outdoors [67]. Species–area relationships, island biogeographical models, and even metabolic theory predict that, as the habitat and resources available in a particular biome increase, so too should its total (gamma) diversity. To the extent that houses vary within and among cities, we might predict that beta diversity is also likely to remain high. We hypothesize that urbanization will increase the number of species that evolve to persist indoors, with the differences among homes, settlements, and regions being a more complex function of the relative differences among them in culture and connectedness.

A trend toward sustainable building practices may also influence indoor evolution. Strategies to improve energy efficiency and control of the indoor biome include tighter

Box 3. Outstanding questions

- Are houses similar enough to consider them a single biome or are they more akin to remote islands (multiple biomes)? Would one expect convergent or divergent evolution to appear across habitats in the indoor biome?
- How will climate change affect both building design and the outdoor environment and, subsequently, determine which species thrive indoors?
- Was there an adaptive evolutionary syndrome of phenotypic or genomic changes that accompanied the evolution of house living in many species in many regions?
- Has evolution of indoor microbes (or colonization by preadapted microbes) influenced our own microbiome health? Can we design buildings to function as healthier human/microbe habitats?
- Are ecological interactions specific or unique in any way indoors or are they analogous to outdoor interactions?
- How many and which species are found exclusively in the biome?
- Have any species moved from the indoor biome to other, outdoor biomes? Is there speciation indoors?
- What is the role of horizontal gene transfer in the indoor biome? How frequent is it and are there indoor hotspots where microbes are more likely to exchange information?
- Are populations of some indoor species genetically distinct within or among different types of structure (e.g., public kitchens versus private kitchens, bedrooms versus movie theaters)? In other words, what is the population structure of the inhabitants of the indoor biome? Does scale matter? Would we be more likely to find structured populations of, say, bacteria than mice?
- What are the primary producers in the indoor biome?
- What can the indoor biome tell us about the origins and formation of other biomes that have existed on Earth?

sealing of building envelopes [68], which has the potential to influence all selection pressures indoors, favoring the subset of lineages that are best able to enter sealed environments and deal with self-contained climate systems [69] and the novel chemistry of new building materials. Although the impacts of sustainable building and new building materials remains to be fully explored, they seem likely to have lasting influences on evolution in the indoor environment – effects we are likely to experience long before they are well studied.

Concluding remarks and future directions

Although many biologists have studied the evolutionary processes at work in indoor environments, such studies focus disproportionately on pest organisms. As a result, most taxa of the indoor biome remain to be considered in an evolutionary ecological framework. As a research field, the evolutionary biology of the indoor biome is interdisciplinary, situated at the intersections of evolutionary biology, ecology, anthropology, archaeology, engineering, architecture and design, human ecology, urban planning, environmental history, and political ecology. There are many avenues open for future research on the ecology and evolution of the indoor biome (Box 3).

Arguably, the indoor biome is one of the realms in which the field of evolution offers the most to humanity. The study of the indoor biome intersects with the field of public health and medicine. Houses with increased levels of fungal, cockroach, and mouse allergens are associated with higher rates of asthma in children, for example, and the absence of beneficial species indoors has been linked to autoimmune and allergic disorders [70]. Evolutionary biol-

Table 1. Categories of species of the indoor biome and references that describe their evolution or ecology in indoor environments

Category	Examples	Refs
Intended introduction	Pets	[78,79]
	Microbes for fermentation	[80,81]
	Houseplants	–
	Humans	[18,82]
Unintended introduction	Human pathogens and parasites	[83,84]
	Arthropods	[30,59,85]
	Human-associated microbes	[57,86,87]
	Other microbes	[22,88–90]
	Rodents	[40,67,91]
	Birds	–
	Bats	[92]
	Other mammals	–
	Reptiles	–

ogists have the opportunity to engage with these basic and applied research topics through the study of indoor biomes.

Perhaps more than any other evolutionary examples, the stories of the species that evolve indoors are accessible to students and other members of the public [71]. Already conservation biologists are engaged in a parallel movement to bring conservation stories to inhabited places [9,72]. Study of the indoor biome could bring evolution to our doorsteps. One framework in which this could occur is through citizen science. Citizen science offers an approach to the study of indoor species that simultaneously engages the public, allows scientists to sample many houses, and generates stories about ecology and evolution of which the public is intricately a part [73]. Recent studies engaging citizens in the study of their own homes have revealed the spread of two species of giant invasive camel cricket among North American basements and crawlspaces [50], patterns of bacterial composition within and among houses [21], and the distribution and composition of ants in backyards [74]. Given that our understanding of the indoor biome remains heavily weighted toward North America and parts of Europe, it will be important to our understanding of indoor evolution to distribute projects more evenly across geographical regions [75].

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