Review

An Ecological and Evolutionary Framework for Commensalism in Anthropogenic Environments

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Commensalism within anthropogenic environments has not been extensively discussed, despite its impact on humans, and there is no formal framework for assessing this ecological relationship in its varied forms. Here, we examine commensalism in anthropogenic environments in detail, considering both ecological and evolutionary drivers. The many assumptions about commensalism and the nature of anthropogenic environments are discussed and we highlight dependency as a key attribute of anthropogenic commensals (anthrodependent taxa). We primarily focus on mammalian species in the anthropogenic-commensal niche, but the traits described and selective pressures presented are likely fundamental to many species engaged in intense commensal relationships with humans. Furthermore, we demonstrate that this largely understudied interaction represents an important opportunity to investigate evolutionary processes in rapidly changing environments.

Why a Framework is Needed

Commensal **taxa** (see Glossary) have been major contributors to the human-mediated biodiversity crisis [1,2], are implicated in zoonoses [3], and were possible sources of domesticates [4,5]; thus, they have a profound impact on life on Earth. However, many aspects of this relationship, and the ecological and evolutionary processes associated with commensal taxa, are surprisingly poorly understood. This stems from the seemingly simple definition of commensalism: a relationship where one species benefits (+) and the other species experiences no impact (0) [6]. Observations of animals benefitting from **anthropogenic environments** often lead to the conclusion that these animals are undergoing commensal-specific evolution. There are many assumptions associated with this evolutionary process, which we break down in this paper. We contend that anthropogenic environments are highly unstable and do not entirely buffer commensal species from seasonality. Therefore, the evolution of commensal taxa is defined by their ability to become dependent on these unstable anthropogenic environments.

Observations of commensal interactions have led researchers in fields such as archaeology and studies of domestication to categorise species as commensally dependent, but without providing a wider ecological context. For example, because there is currently no adequate ecology-based framework for commensal evolution, the view that feral dog populations are reasonable models for 'proto-domestic' forms (e.g., [4,7]) has not been assessed with sufficient rigour. The assumption that domestic dogs derive ultimately from commensal wolves, therefore remains a premise underpinning much of the research into dog domestication (e.g., [8]). Although wolves

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do engage in commensal relationships with humans as **facultative scavengers** (e.g., [9]), whether it is possible for a subgroup of wolves, prior to direct human interaction, truly to become a commensal taxon in the evolutionary sense remains untested.

A New Framework: Anthrodependent Taxa

A review of the current usage of the term 'commensalism' in anthropogenic environments highlights how dependence is central to the understanding of commensal taxa. Here, we identify the unpredictability and instability of the anthropogenic niche as the primary selective pressures involved in the evolution of commensal species. Furthermore, we demonstrate that an ecological framework is required to: (i) identify the intensity of the relationship in order to define a taxon as commensal; (ii) assess the complexities of ecological systems associated with commensals; and (iii) assess selective pressures on commensal taxa that drive their evolution. We propose a new term for organisms that might represent the typical commensal condition in an anthropogenic environment: 'anthrodependent taxa' or 'anthrodependants' (Box 1).

A Not So Simple Relationship

The term 'commensal', denoting a relationship, has a straightforward meaning [6]. However, when the term is applied to a taxon (e.g., to rodents [10] or to a so-called 'proto-domestic' species [4]), it often means something more complex, reflecting both the acquisition of a new capability to exploit the anthropogenic environment and an associated reliance upon it. Furthermore, as the relationship becomes more intense (one of dependence), these 'commensal

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Box 1. Previously Used Definitions of Species in Anthropogenic Environments (with Our Proposed New Category*)

Commensal taxa (com-: sharing and -mensa: table)

Commensalism in its original and simplest form specifies a relationship, represented as +/0, whereby one organism benefits (+) from another without causing deleterious effects to the other (0) [6]. As applied to taxa, rather than relationships, it often refers to species living within houses [10,12]. More precisely, 'true commensals' live entirely in houses, 'occasional commensals' move between houses and outdoor habitats, and 'obligate commensals' are those that can only survive in an area because of their ability to occupy houses (e.g., black rats in northern Europe).

Synanthropic and synurban taxa (syn-: together)

These terms are used in studies of species that continue to live in areas that are occupied and altered by humans [83,84]. They can include both obligate-commensal species and also species not dependent on, or even particularly benefiting from, humans [83]. These synanthropic species show a changed lifestyle associated with living in close proximity with humans (affecting breeding cycles, territorial behaviour, foraging behaviour, diet, etc. [85,86]). Synanthropic is also used to describe proto-commensal species in archaeology (e.g., [87]).

Anthropophilic taxa (-phile: lover of)

Traditionally applied to ectoparasites, this term has increasingly been used in archaeology to indicate species attracted to human environments and activities [4,88,89]. This can include not only commensal species, but also species opportunistically benefitting from humans, without dependence [90].

Domestic taxa (domus-: house)

Humans actively buffer these taxa from external selective pressures, enhancing survival, and breeding. Therefore, humans reduce and sometimes remove impacts of natural evolutionary processes on these taxa and, at more advanced stages of domestication, humans directly control the selective pressures.

*Anthrodependent taxa

We propose this term to refer to those taxa that might have had, and continue to have, a commensal relationship (+/0), but are defined by their dependence on anthropogenic resources, which in some cases can have a negative impact on their once commensal partner.

Glossary

Adaptation: an evolutionary process whereby organisms become better suited to the environments they occupy.

Anthropogenic environment: an environment that is created and maintained by humans, such that natural fluctuations and seasonal changes are altered.

Community composition: the range of species that comprise a community of organisms in any given environment or ecosystem.

Facultative scavenger: an animal that occasionally and opportunistically partakes in scavenging; they are not dependent on scavenging for survival.

Home range: the area regularly travelled by an animal as part of its routine behaviour (i.e., foraging, feeding, sleeping, and mating).

Natural environments: environments where species use the environment and fluctuate in numbers in a way expected in the absence of or under little influence from humans (noting that almost all environments are now influenced by humans)

Plasticity: a response to changed environment or circumstances that is not fixed by the biology of the organism (i.e., by its genotype or anatomy). This can include not only behavioural changes in animals, but also physical changes due to changes in development in response to environment. A plastic response might be a first stage in adaptation.

Selective pressure: the extent to which traits are favoured (selected for) or disfavoured (selected against) in any given environment, resulting in adaptation (see above).

Taxon (plural: taxa): an evolutionary unit, such as a species, family, or order.

Box 2. The Nature of a Relationship: 'Commensal Neutrality'

Many so-called 'commensal' species have anything but a neutral relationship with humans [3]. Their role as disease vectors might be considered a key negative impact [11], but it is entirely indirect, given that essentially no energy is expended to spread the disease (although parasite-induced behaviours exist [91]). Competition for resources is understood to be a–/–relationship [6], with more obvious direct interaction. However, the comparison between the impact of disease and the damage from competition is difficult to quantify and might suggest that, when present, the indirect pathogen impact has a greater and more acute effect than the direct competition resulting from crop consumption [3]. Also, should we take into account the ability of humans to mitigate such impacts when considering whether a relationship is largely neutral or otherwise? Another question that is raised by the quantification of interactions is whether negative interactions are overriding and additive or whether they can be balanced by beneficial activities. Feral cats are a possible commensal species; they carry toxoplasmosis, a disease known to affect humans [91], but they also consume and regulate populations of other species known to carry many more diseases [11]. Feral cats consume competitors of humans (rodents), so if disease is not considered, does that then make the relationship mutual? Does the perceived beneficial behaviour of feral cats mitigate the negative impact they can have on humans? Ultimately, this extremely complex set of impacts affects the evolution of all organisms involved but, on an evolutionary ecology scale, it is currently unquantifiable. As a result, it might be best to simply categorise these interactions as fluctuating and complex rather than trying to define them as negative or neutral.
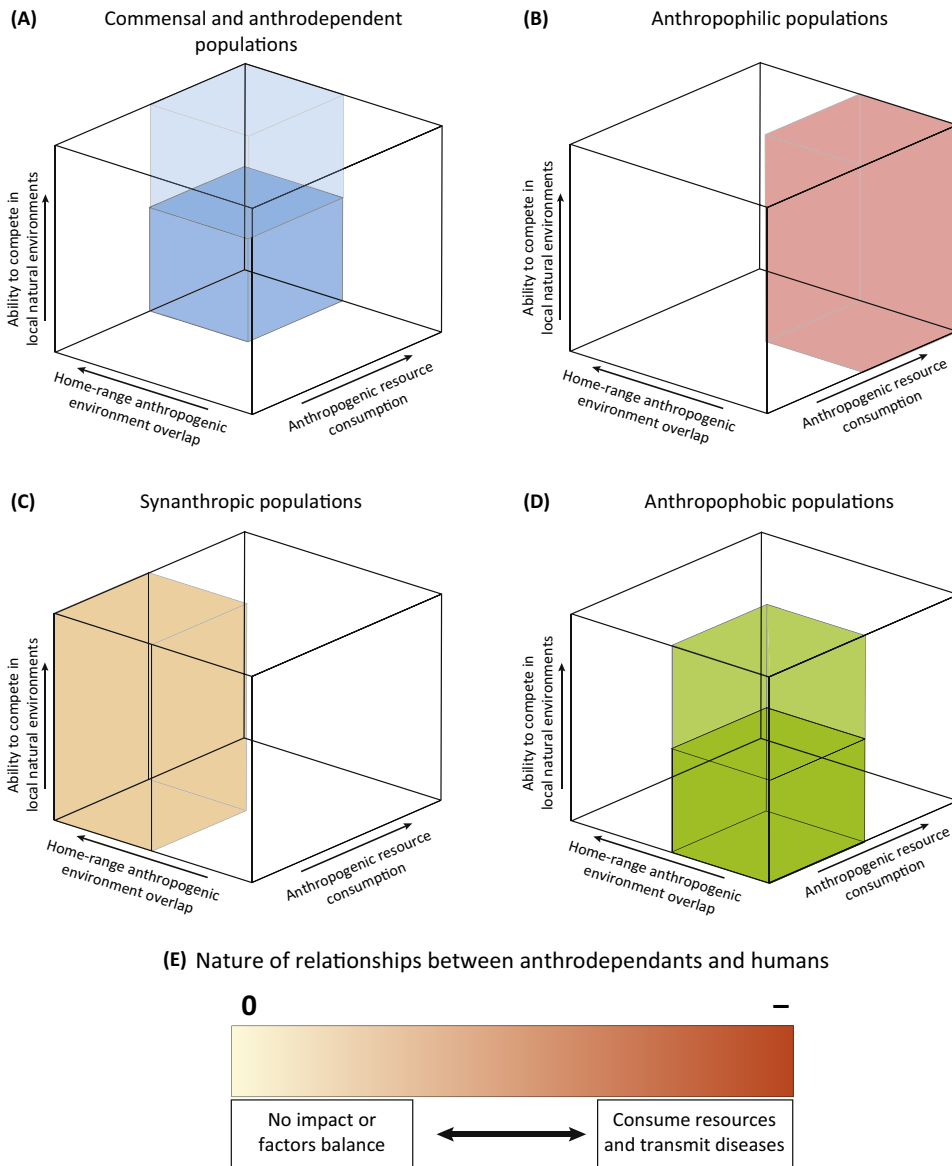
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taxa' rarely have a neutral impact on humans; for example, they consume crops, steal food, and/or harbour disease [3,11] (Box 2).

Taxa categorised as 'commensal' are reasonably assumed to be exposed to selective pressures relating to their exploitation of the anthropogenic niche [12]. However, just what the main characteristics of the anthropogenic niche are (beyond a simplistic view that it represents a concentration of resources associated in some way with humans) remains unexplored, and this has led to further broad assumptions being made about evolutionary pressures on proposed commensal taxa (e.g. [8]). Beyond the obvious settings of human-made structures and urban environments, it must also be recognised that agricultural environments are also subject to unpredictable and unseasonal human activity, resulting in 'unnatural' availability of resources. These too have a range of associated dependent taxa, often considered 'pests'. At low densities, such taxa might be considered to hold commensal relationships, but, as densities become higher, they might be viewed as competitors, although these categories are largely subjective. From an ecological and evolutionary perspective, these competing taxa inhabit an unpredictable and fluctuating anthropogenic environment similar to that experienced by many commensals and, therefore, can be considered anthrodependent with a commensal origin.

The Need for a Scalable Term

Other discrepancies in definitions stem from a research bias towards small-bodied animals living in human-made structures [10,12]. Occupation of such structures sets an arbitrary definition of 'commensal taxa' with the result that comparisons of similar evolutionary processes experienced by large-bodied species are overlooked. In this way, a unifying definition and understanding is needed of 'commensal taxa' that allows an evolutionary understanding and is transferable between taxa (with varying body and **home-range** sizes) that occupy different anthropogenic environments and exploit diverse anthropogenic resources.

Far more useful is to consider commensalism (and other related types of species interaction) in terms of the degree of dependence upon an anthropogenic niche (Figure 1). Dependency comes with both benefits and costs, which in turn drive the evolution of anthrodependent taxa [5]. Examining the selective pressures stemming from both benefits and costs provides a more appropriate framework that allows detailed insight into evolutionary processes specifically associated with past, present, and future anthropogenic environments. Only by interrogating the archaeological record will we gain a fuller understanding of the way such taxa evolve and adapt [13].

(A) Commensal and anthrodependent populations

(B) Anthropophilic populations

(C) Synanthropic populations

(D) Anthropophobic populations

(E) Nature of relationships between anthrodependants and humans

Figure 1. The Way in which Species Interact with Anthropogenic Environments is Best Considered at a Population Level. As a result, different populations of the same species can hold different positions within this conceptualised schematic of interactions with anthropogenic environments. (A) The dark-shaded cube represents obligate-commensal populations that are wholly dependent on anthropogenic environments, while the lighter cube represents commensal populations that are competitively capable in natural environments. (B) Anthropophilic populations include facultative scavengers, which regularly consume anthropogenic resources but display behaviour to suggest they are not wholly dependent on humans. (C) Synanthropic populations have home ranges that overlap extensively with anthropogenic environments but otherwise do not interact greatly with anthropogenic resources. (D) Anthropophobic or natural populations avoid home-range overlap with humans and do not consume human resources. The lighter cube might be considered natural specialists, while the dark cube are natural generalists. (E) The new category of commensal taxa that we propose, anthrodependants, can affect humans in different ways; weighting the negative and positive impacts might be difficult. Here we propose how anthrodependent taxa might fall on a scale.

The Anthropogenic-Commensal Niche

Humans have been actively altering the environment around them for thousands of years in what can be considered a form of niche construction [14]. It is this constructed environment, and the abundance of resources within it, to which anthrodependent taxa have adapted and thrived. The extent of anthropogenic environments has increased through time [14], as has the prevalence of commensal taxa [15]. The ability of a taxon to maintain access to anthropogenic environments dictates its success and evolution as an anthrodependant. In particular, this environment is often characterised by extreme and unpredictable fluctuations of resource availability and nest sites [12,16], characteristics that are frequently overlooked.

Costs in Anthropogenic Environments: Why Storage Does Not Mitigate Seasonality for Anthrodependants

It is often assumed that anthropogenic environments are more stable in terms of resource availability than are **natural environments** [17]. This is not always the case [12]; neither was it likely to have been so throughout the past, when wild organisms first entered the anthropogenic niche [13,15,18]. Humans radically modify their environment at frequent intervals, amplifying the seasonal variability of agricultural landscapes and quickly changing urban settings in unpredictable ways (Box 3).

Agricultural resource availability is tied to seasonal cycles and associated processes, such as harvest, storage, and trade (e.g., [19]). These factors rapidly accentuate and then dramatically deplete resource availability. Harvesting results in rapid depletion and relocation of resources, while storage leads to their mass concentration. Other more complex sociocultural factors (e.g., trade or conflict) can even remove the resource entirely and unpredictably (e.g., [20]). For humans, these factors (combined with social distribution networks) help to mitigate seasonal fluctuations in resource availability. The converse is true for anthrodependants (particularly on a local scale) where these factors create an unstable and fluctuating environment that affect animals of varying body sizes and differing generation times in different ways. For example, a small number of house mice (*Mus musculus*) occupying an empty barn and feeding on resources in neighbouring areas must have the behavioural plasticity to compete and survive when there is a mass influx of the same or other species during periods of storage. Therefore, although agriculture and storage might appear to alleviate fluctuations in the environment, they

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Box 3. Fluctuating Resources

Human activity in the landscape greatly alters the normal seasonal cycle of resource availability, in both agricultural and urban environments. How these fluctuations quantitatively compare with natural environments shapes selective pressures on commensal species. Within urban environments, refuse from humans provides a regular source of food [92]. For example, per person per year in New York City, people drop approximately 2.6 kg of food litter in the streets [76] and household food waste is recorded to be a minimum of 50 kg per person per year [93], an unknown proportion of which is consumed by commensal species. From agricultural environments, cereal production at harvest is carefully recorded (e.g., by the World Bank[i]), and studies estimate both pre- and post-harvest consumption of cereal by 'pest' species is on average 5–15% (e.g., rodent damage [3]). Within natural environments, data for mast-fruiting years versus non-mast-fruiting years are available for various tree species (e.g., beech [94] and oak [95]), as one specific example of a natural food source for rodents. In non-mast years, fruit is scarce by January, whereas during mast years, stores of fruit last through the winter until the following summer. Mast-fruiting allows year-round breeding for some species of rodent [95]. As a generality, we suggest resources fluctuate as follows:

- Urban (Figure IA): these environments used to vary substantially between settlements but have been stabilising over recent centuries; have greater availability of food than either agricultural or natural environments; produce a constant level of food waste; and can be unpredictably and rapidly depleted at a local level.
- Agricultural (Figure IB): these environments used to vary substantially between regions but have been stabilising over recent centuries; accentuate seasonal variation between superabundance and complete scarcity; produce more food than natural environments; and diversity of crops and/or biodiversity is low, which results in shorter periods of resource availability.
- Natural (Figure IC): these environments are highly variable between habitats; seasonal variation is generally predictable; mast fruiting (and other large-scale availability of food) occurs occasionally; and catastrophic fluctuations occur infrequently.
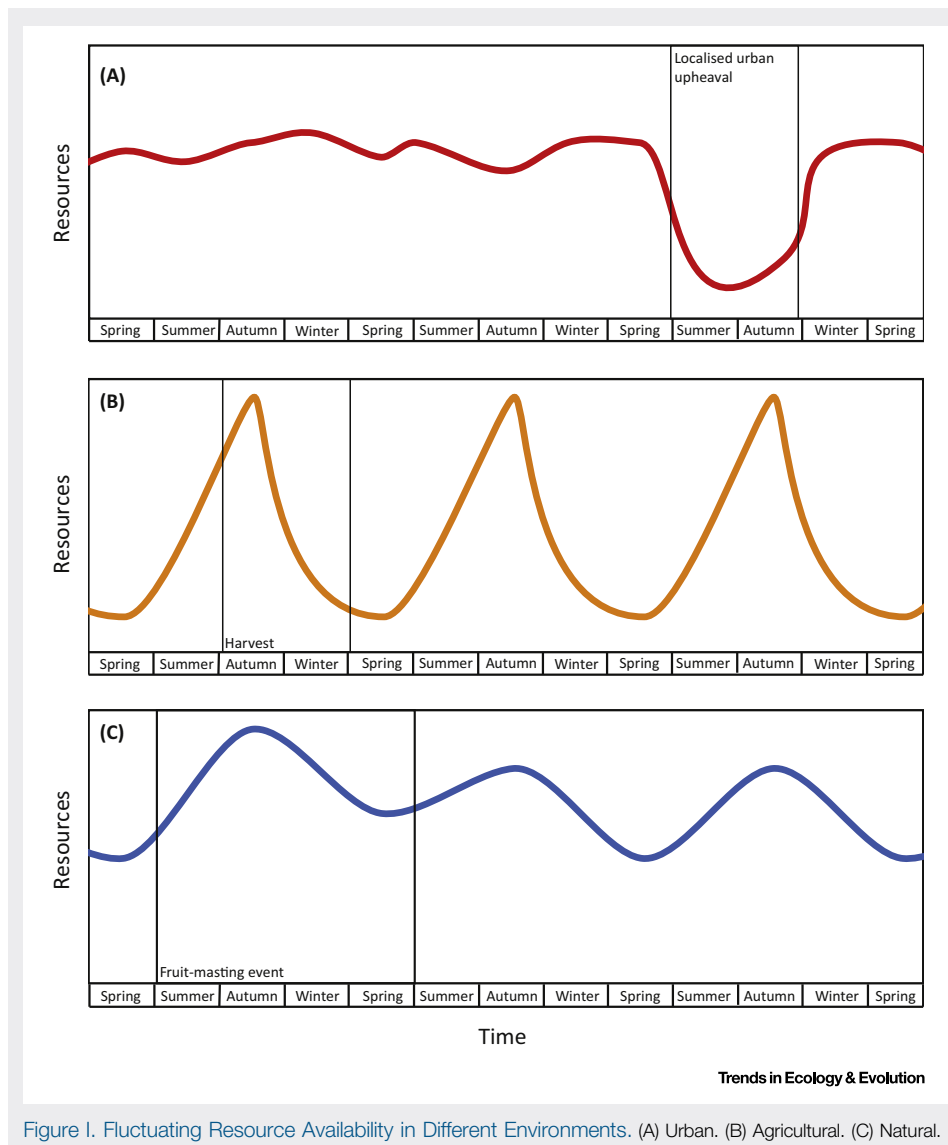
Figure I. Fluctuating Resource Availability in Different Environments. (A) Urban. (B) Agricultural. (C) Natural.

can also exacerbate them from the perspective of organisms that maintain territories, have small home ranges, and fare poorly under inter- or intraspecific competition.

Resource Fluctuations in Urban Environments

Equally, urban environments have unnatural resource availability. Although resources are likely available in superabundance across seasons, physical and social changes (e.g., due to building technology, urban decay, urban redevelopment, waste management, and differences in socio-economic waste production) can rapidly deplete once superabundant resources [2,20–22]. By contrast, in natural environments with greater biodiversity, resources become available season-ally. Therefore, species occupying anthropogenic environments (whether agricultural or urban) need specific traits to cope with such dramatic fluctuations in resources.

Accessing Anthropogenic Resources

Occupation Does Not Equal Dependence

If anthropogenic environments have abrupt boundaries, commensal taxa are unlikely to recognise them. Animal inhabitants of gardens and farmland interact with human resources

(e.g., refuse and agricultural produce) to differing degrees. Therefore, existing definitions of commensal taxa that are based on occupation of human structures are likely to be inappropriate (e.g., [12]). They do not denote dependency (e.g., kestrels roosting in buildings are not dependent on those buildings [23]) and they are restricting when examining comparable evolutionary processes. How commensal taxa interact with and behave while accessing anthropogenic resources (e.g., home-range size, territoriality, and movement) provide far greater insight into their evolution.

Changing Mobility Patterns: Rodents and Foxes

A regular observation is that individuals within commensal urban populations have reduced home ranges compared with members of rural populations, likely reflecting relative food availability [24–26]. House mice, the archetypal commensal species, can live at extremely high densities and often exclusively occupy human-made structures within urban environments [12,25]. However, there is good evidence that crop harvesting leads to the migration of house mice from agricultural environments to storage and urban areas [25], and even woodland habitats [27]. Therefore, with movement and shifts in home range, urban, rural, and agricultural populations can all act as source populations, and selective pressures on one group can affect others.

Large rodent species capable of dispersing substantial distances [e.g., the brown rat (*Rattus norvegicus*)] also have smaller home-range sizes in anthropogenic compared with natural environments [24]. Similar to commensal mice, many rat species migrate and travel long distances to exploit anthropogenic resources [27]. Farmland populations of brown rats can be highly dependent on anthropogenic resources, with nightly tracking data showing individuals travelling 3–6 km to feed at refuse sites [28]. Although these animals would not be considered commensal using a definition of proximity, if we recognise that the environment and resources they depend upon are unpredictable and determined by human activity, they can then be considered anthrodependent or commensal taxa. Considering them in this way gives us insights into their evolution and success.

The red fox (*Vulpes vulpes*) represents a larger-bodied candidate for consideration as a commensal species [29,30]. It too shows substantial variability in home-range size between natural, rural, and urban areas [31]. Urban foxes often have den sites located on the peripheries of their home ranges, with nocturnal territories that include urban areas where they feed [32,33]. This occurs particularly where humans are intolerant of fox activity [33]. Therefore, urban foxes are an example of an animal dependent upon refuse and associated vermin, but that often do not occupy den sites within human settlements or structures.

Occupying but not Dependent

Dependency on anthropogenic resources remains a key distinction between commensal taxa and taxa that might be considered synanthropic or anthropophilic because they occasionally hold a simple commensal (+/0) relationship. Garden bird species are synanthropic and occasionally anthropophilic, but do not necessarily depend on the anthropogenic environment since they move freely to and from neighbouring natural habitats {e.g., European blackbirds (*Turdus merula*) [34] and blue tits (*Cyanistes caeruleus*) [35]}. Some of these species show plastic responses to anthropogenic environments, but these might not constitute dependency (e.g., song pitch when exposed to traffic noise [36–38]). The point at which such traits drive organisms to become dependent commensals is only now being realised and explored. For example, changes in reproductive cycle and sedentism in urban- and forest-living European blackbirds indicate local adaption to urban microclimates [34]. These urban blackbirds deposit lower levels of fat than their forest-living counterparts, making them less suited to migration, but allowing them to reach sexual maturity more quickly [34]. In this instance, it could be argued that a

synanthropic species is developing into an anthropophilic one, which might eventually become an anthrodependent species.

Benefits versus Costs and Competition in the Commensal Niche

For anthrodependent taxa, exploitation of anthropogenic resources cannot be thought of only in terms of benefits, because, with dependency, the organism is subject to many costs. Examining benefit versus cost provides evolutionary insights [12].

Community composition of commensal small mammals across the urban–rural–wild gradient demonstrates differences in the ability of species to compete with each other [39]. Variation in community composition of commensal species in human settlements over the long term illustrates how changes in building materials and storage practices favour some species over others {e.g., changes from wood to concrete correspond with changes in prevalence of three major commensal species: the arboreal black rat (*Rattus rattus*); the fossorial brown rat; and the crevice-dwelling house mouse [40]}. This intense competition in highly fluctuating environments results in high population turnover [24,41–43]. Therefore, the benefits offered by the occasional superabundance of resources are offset by the unpredictability of the environment they occupy and the constant and rapid change in levels and type of competition associated with accessing those resources.

Colonisation of Anthropogenic Environments

Invasive Processes

Commensal species living in anthropogenic environments are analogous to invasive species colonising and occupying new locations. The growing discipline of invasive biology seeks to identify and then model common traits among invasive species. Fluctuating and disrupted environments, with unexploited or superabundant resources, are particularly prone to invasion [44,45] and such characteristics are also common to anthropogenic environments. Furthermore, following disruptions in anthropogenic environments, anthrodependent species recolonise habitats similarly to invasive species colonising new environments. Invasive species are generally rapid breeders with high mortality and short longevity, characteristics that help mitigate against small founding populations [46,47]. The most successful invasive species are consumers and occupiers of multiple lower trophic levels [48]. Commensal taxa fit perfectly with this description.

Invasive Does Not Equate with Anthrodependent

Most (if not all) commensal species are already considered highly invasive and, as such, have driven studies on the theory behind invasive biology. They often become invasive in non-commensal environments when competition is low and resources are unexploited (e.g., rats on Pacific islands [49]). However, not all invasive species are commensal; there are multiple invasive species that were deliberately introduced as human food sources, for pest control, or for aesthetic reasons, among others. These invasive species have little natural inclination to avail themselves of anthropogenic resources (e.g., small Indian mongoose [50], stoat [51], camel [52], or European rabbit [53]). Studies have examined how exotic species of varying competitive abilities successfully colonise, with the introduction stage found to be most critical [44,54,55]. These processes are also particularly important to the success of commensal species.

Trait Selection Driven by the Commensal Niche

Recolonisation Is Key

In a highly fluctuating environment, with intense competition and rapid unpredictable change, anthrodependent taxa frequently repopulate or recolonise local environments. Therefore, fecundity dictates the success of these taxa because they must continually rebound from low numbers in a way that is comparable with the founding stage of invasion [56–58].

Anthrodependent taxa generally conform with what are considered r-selected traits, with high levels of fecundity, rapid sexual maturity, and catastrophic mortality [47]. Although r/K-selected traits are a simplification of reality [59], the extremes of abundance and fluctuations in anthropogenic environments lead to an environment best suited to species that fit the paradigm of r-selection.

House mice are a perfect example; with year-round breeding and large litters [60,61], they show high levels of mortality and widely fluctuating population sizes. Unsurprisingly, some of the most successful commensal taxa (e.g., rats [2]) are also generalist omnivores and display a propensity for novel feeding behaviour, dietary plasticity, and consumption of a range of lower trophic-level resources [62], traits also predicted by food-web modelling of invasive species [63].

Coping with High Density

High population density characterises occupation of anthropogenic environments by commensal species [25]. This high population density requires plasticity of territorial behaviour (Box 4) and nest-site selection [57]. Commensal taxa, such as house mice, display a range of different

Box 4. Territorial Behaviour

With fluctuating availability of resources, commensal species that do not typically form fixed feeding territories would be expected to be at an advantage. When resources are in superabundance and populations reach correspondingly high density, commensal rodents can exhibit territorial behaviour, thereby monopolising resources [12]. However, this behaviour is plastic and, at low density, territories dissipate [12]. Behaviour will vary between species in the commensal niche, but maintaining foraging mobility is likely to dictate the viability of a commensal population and it should not be assumed that commensal species are highly sedentary (e.g., urban fox [32,96] or brown rats [28]).

Feral cats and dogs demonstrate the importance of territorial behaviour in a commensal setting. Feral dog populations in the commensal niche (particularly those comprising strays and their offspring) display both feeding and breeding territorial behaviour (Figure IA), but show little within-group cooperation or social organisation [9]. Consequently, resource exploitation is poor, breeding is extensive, and pregnant females and pups receive no preferential access to resources [9]. These populations are only maintained by recruitment of new strays [9]. Conversely, the most successful commensal feral cat populations show a different set of behaviours: social dominance is maintained based on individual interactions; group living is maintained, and territorial behaviour is not shown within the group [97] (Figure IB). Young and pregnant females are given priority access to food and shown greater tolerance [97]. These examples of feral commensal populations provide models for further investigation into the effects of behaviour on species occupying a commensal niche. The different strategies of feral dogs and cats might be successful under different circumstances, according to the rate of interloper influx and level of resource availability. Exploring the circumstances under which species can be successful commensals will provide ways to assess the feasibility of the commensal pathway to domestication for these species. Furthermore, exploring such dynamics can help explain why some small mammals identified as ancient commensals (e.g., species within the Cricetidae and Soricidae [15]) were later outcompeted by what are now modern commensal species (e.g., house mice).
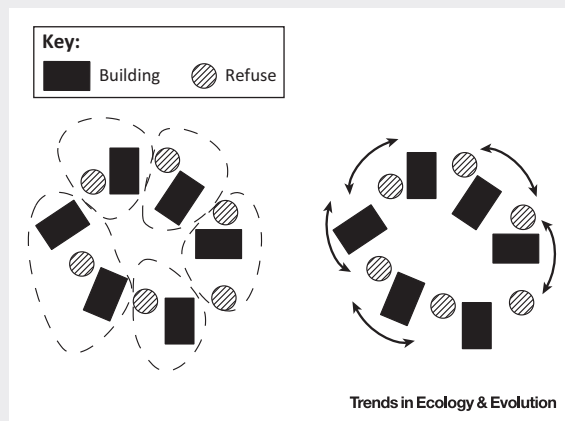

Figure I. Territorial versus Nonterritorial Behavioural Strategies. (A) Territorial: with individuals having static defended home ranges (broken lines); (B) nonterritorial: with individuals having high mobility (arrows).

behaviours at different densities, from nomadism at low density to the formation of male-dominated territories at high density [12]. Similarly, urban foxes adopt group living behaviour at high density [64]. Solitary species (or those that cannot live at high density due to territorial behaviour) are unlikely to fare so well in fluctuating anthropogenic environments. Behavioural traits, such as group foraging and feeding plasticity, are also highly advantageous (e.g., as observed in brown and Pacific rats [65,66]).

Genetic Signals and Selective Pressures of the Commensal Niche

Investigation of changing selective pressures on commensal taxa can be explored through identification of discrete genetic markers through time, and this is where detailed interrogation of the archaeological record (specifically ancient DNA) will prove invaluable. However, it is unlikely traits will be identifiable as monogenic, since many loci are more likely involved. As a result, genome analysis of commensal species (incorporating archaeological material where possible) will provide the most robust and explicit evidence for **adaptation** to commensalism.

Rapidly Changing and Localised Selective Pressures

Anthropogenic environments have changed dramatically through time, from a mosaic of different crop types and building methods [67] to modern homogeneous building styles [2] and large-scale mono-cropping [68]. Therefore, it is likely that any genetic changes linked with adaptations to the commensal niche might vary between localities, reflecting regional human behaviours, cultures, and technologies [2]. However, many synanthropic or anthropophilic taxa will experience similar local selective pressures as those that affect commensal taxa, so specific genetic signals might not be exclusive to commensal species. Therefore, analyses incorporating change through time will be important to distinguish between different categories of taxa associated with anthropogenic environments.

Many of these adaptations are currently better known from synanthropic and anthropophilic species than for commensals. These include immune system responses in high-density populations [69], resistance to pollutants and poisons [70–72], and dietary [8] and behavioural changes (e.g., to superabundance of food and high-density populations [73]). Other traits specific to the commensal niche (such as those associated with fecundity) will likely be selected for, but many will not be monogenic. Genetic variants associated with sperm quantity and quality will likely be strongly selected for from the earliest development of intense commensal dependence due to high population densities (e.g., [74]), an aspect worthy of further investigation.

Effects of Human-Mediated Dispersal

It should also be expected that commensal species (particularly those of small body size) are likely to exhibit increased levels of gene flow (where populations are linked through human transport) than the same or similar species occupying natural environments [75]. Due to these same transport networks, and the resulting regularity with which commensal species are introduced to new regions and environments, it is likely that most commensal populations are exposed to intense selective pressures relating to local environments and climates (e.g., introduction of tropical *R. rattus* to temperate climates of northern latitudes [3,49]). As a result, examining commensal genomes through time will also provide insights into adaptive responses to rapid climate change.

Degrees of Separation: Commensal Carnivores and Insectivores

The ability of highly carnivorous species to occupy and depend on a commensal niche raises a particularly interesting set of questions. With commensal populations reaching high densities in man-made environments, other taxa can also exploit that niche by predating them. Since these predators are dependent on this anthropogenic niche, they should (by extension) be considered anthrodependent taxa by a degree of separation. They benefit from the superabundance of prey

in anthropogenic environments and (as their prey fluctuates) experience the costs of dependence on anthropogenic resources; as a result, they likely undergo similar selective pressures to anthrodependants. For example, anthropogenic habitats also attract many arthropods [76], which are readily consumed by insectivores {e.g., the Asian house shrew (*Suncus murinus*) [77]}. This species is generally regarded as commensal due to their occupation of houses, but they also exhibit a similar suite of traits to other commensals to maintain dependency on this niche [78]. By contrast, urban foxes are generally considered facultative scavengers, but they also hunt other commensal taxa and, as previously demonstrated, might also be considered anthrodependants [79].

Commensal relationships between humans and carnivores, in the form of facultative scavenging, certainly do exist (e.g., wolves scavenging refuse [80]). In some cases, carnivores (e.g., cats [81]) might be highly dependent on hunting other commensal species. This has been a particular focus of archaeological endeavour, specifically in studies where commensalism is proposed as an important pathway to animal domestication [4,5,8,81]. Assessing the intensity of that commensal relationship through early prehistory will be important to establish whether those relationships were opportunistic (and, therefore, anthropophilic), requiring direct human involvement to transition to domestic, or whether the anthrodependent taxon evolved to an intermediate ('proto-domestic') stage.

Concluding Remarks: Changing Face of Commensalism

A dependency on anthropogenic environments can be considered the best indicator of commensal status for taxa. The onset of what is considered the Anthropocene demonstrates the importance of understanding the human role in creating and influencing environments [82], the nature of which needs further investigation. Which mammalian species comprise the dominant commensal and 'pest' species (i.e., black rats, brown rats, and house mice today [3]) has the potential to change rapidly, depending on changes in agricultural technology, building technology, and climate, and this should be explored through a deeper temporal context with the archaeological record. As anthropogenic environments become globally more homogeneous, they might enter a new, more stable phase, where specialists can start to appear. However, for the moment, those species that can breed rapidly, live at high density, and are generalist omnivores appear to have the greatest advantage.

There is great potential for advancing our understanding of multiple aspects of ecological and evolutionary processes through the comparative study of modern and archaeological commensal taxa and other types of analysis (see Outstanding Questions). Commensal taxa represent a unique tool with which to investigate intense selective pressures on species in rapidly changing environments.

Resources

[i] http://data.worldbank.org

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Outstanding Questions

There is insufficient discussion about commensalism in anthropogenic environments and, although such environments are attracting increasing interest (e.g., [7,61]), unwarranted assumptions are often made about them.

We have primarily focussed on mammalian examples of commensal species. For other groups (e.g., arthropods, birds, and herptiles), are the selective pressures and traits required similar?

How do fluctuations in natural and anthropogenic environments compare?

How stable were anthropogenic environments in the past, how stable are they now, and how stable will they be in the future?

Do the selective pressures associated with dependency on urban and rural environments have commonalities and how do commensal and 'pest' species respond to them?

How has the commensal community composition changed over time and can we predict how it might change in the future?

What can community composition of past anthropogenic environments tell us about those environments?

How intense were the commensal relations between our ancestors and proto-domestic species and what are the implications for the current domestication hypotheses?

What are the generalities in terms of behaviour (especially wariness) of commensals and how does that relate to the current domestication hypotheses? Could differences in wariness behaviour be tested in different wild strains of model species (e.g., brown rats and house mice)?

Over time, do adaptive plastic behaviours exhibited by synanthropic taxa predispose to genotypic changes, thereby reinforcing their dependence on anthropogenic niches?

What can the commensal species model for evolution in rapidly changing environments tell us about adaptations to dietary change, pollution, and climate change?

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