Trends in
Ecology & Evolution

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Opinion

Understanding human-commensalism through an ecological and evolutionary framework

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Human-commensalism has been intuitively characterised as an interspecific interaction whereby non-human individuals benefit from tight associations with anthropogenic environments. However, a clear definition of human-commensalism, rooted within an ecological and evolutionary framework, has yet to be proposed. Here, we define human-commensalism as a population-level dependence on anthropogenic resources, associated with genetic differentiation from the ancestral, non-commensal form. Such a definition helps us to understand the origins of human-commensalism and the pace and form of adaptation to anthropogenic niches, and may enable the prediction of future evolution in an increasingly human-modified world. Our discussion encourages greater consideration of the spatial and temporal complexity in anthropogenic niches, promoting a nuanced consideration of human-commensal populations when formulating research questions.

Highlights

Human-commensalism has been used to broadly describe interactions in which non-human partners benefit from tight associations with humans and their environments.

Human-commensal status has often been intuitively assigned, and the term has been applied without first being clearly defined. This has led to inconsistencies in application across different fields and confusion with other ecologically distinct descriptors of human association.

We propose a clear definition of human-commensalism rooted within an ecological and evolutionary framework. Such framing enables exploration of the potential origins of human-commensalism and has implications for the study of biogeography and demography, the pace and form of adaptation to an anthropogenic niche, and predictions of future evolutionary change in response to anthropogenic pressures.

The need to define human-commensalism

Humans have acted as **niche constructors** (see Glossary) since the Late Pleistocene [1,2]. Through development of fixed settlements, agricultural practices, transportation networks, and energy infrastructure, humans have directly or indirectly modified 95% of the Earth's land [3]. The introduction of anthropogenic selective pressures has had varying impacts on the ecological and evolutionary trajectories of species across different spatial and temporal scales [4–6]. For many species, increased human activity has been associated with population size reductions, extirpations, or extinction [7–10]. For others, trait modification, either via phenotypic **plasticity** or **adaptation**, has enabled persistence in **human-modified environments** [11]. A small number of populations have even benefitted from increased human association, with some evolving a dependency upon **anthropogenic resources** [12].

The term 'human-commensal' has been used to broadly categorise a subset of non-human taxa that benefit from tight human association [13]. Without a rigorous definition, human-commensal status has been somewhat intuitively applied across a variety of taxonomic groups, including amphibians [14], birds [15–19], insects [20–22], primates [23–25], plants [26], and rodents [27–29]. Human-commensalism has also been referenced in multiple ecological contexts, including the study of commensal pathways to speciation and domestication [30–33], dispersal and phylogeographic dynamics of pests [29,34] and disease vectors [27], and phenotypic [35] or genomic [36–38] adaptation to human-modified habitats. Human-commensalism is therefore of ecological and evolutionary interest, but the term's utility is limited by the lack of a clear definition.

Modern understanding of human-commensalism extends beyond the classical cost–benefit frameworks associated with the term 'commensalism' (Box 1). Human-commensalism is now

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Box 1. Human-commensalism and associated terminology

Commensalism

Commensalism classically describes a symbiotic pairwise interaction in which one partner benefits (+), through acquisition of resources, nutrients, shelter, or facilitation of locomotion, whilst the other experiences no net benefit or harm (0) [13,45]. Based on traditional definitions alone, human-commensalism may be assumed to represent a species-specific extension of this +/0 framework, where non-human partners benefit from exploitation of human-modified environments [13].

Describing human-commensalism purely using a classical cost–benefit framework is an oversimplification. Interactions between humans and their commensal counterparts do not necessarily lead to, respectively, neutral or beneficial outcomes [13,45]. Rather, the consequences of human-commensalism vary over space and time. Previous applications of human-commensalism have been criticised for failing to account for the costs of a human-commensal strategy during human disturbance events [79], the negative effects of human-commensals that act as disease vectors [27], and the philosophical limitations of proving a total absence of interaction consequence for human partners [80]. However, these issues are largely addressed by specifying that cost and benefit, when considering human-commensalism in an evolutionary framework, should be assessed solely on the basis of fitness effects. This means the fitness benefit to the non-human partner is much larger than the net fitness effects imposed on the human partner.

Anthropophilic, synanthropic, synurbic

Several terms have recently been introduced, particularly within the urban ecological literature, to describe the strength of relationship between humans and non-human interactors. Examples include 'anthropophilic' (attracted to human-modified environments) [12,32], 'synanthropic' (living in and benefitting from human-modified environments but without a dependence on anthropogenic resources) [39], and 'synurbic' (a special case of synanthropy representing adaptation to urban environments) [40,41]. Whilst these terms usefully illustrate the variability in the extent to which populations interact with human-modified environments, their application could become problematic if each is treated as an arbitrary stage on a single trajectory towards human dependence. Due to the spatial and temporal complexity of anthropogenic environments [12], it is unlikely that there is a single route for populations to transition from no human association, through synanthropy, to human-commensalism. Furthermore, it should not be assumed that a currently synanthropic population will ever evolve to become human-commensal, although this remains possible, or that human-commensalism represents some form of fixed endpoint on a continuum of human association. Application of these terms may also cause confusion when each is used interchangeably (e.g., describing a single population as synanthropic and human-commensal). These terms are not synonymous and should be applied cautiously. Terms such as anthropophilic, synanthropic, and human-commensal are linked, and clearly useful in their own rights, but should always be referenced with complete definitions to avoid misinterpretation.

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most synonymous with anthrodependence [12], a term that is relatively well defined yet far less entrenched within the literature. More broadly, human-commensalism tends to be grouped with terms used to demarcate stages on a continuum of human interaction intensity (including 'synanthropic' [39], 'anthropophilic' [12,32], 'synurbic' [40,41], and 'urban exploiter' [42,43]) (Box 1). As many of these terms, including human-commensalism, have not been explicitly linked to their underlying mechanisms, it is challenging to incorporate the different forms of human association into predictive frameworks. Inconsistent use of terminology has resulted in ambiguity in how human-commensalism differs functionally and mechanistically from other anthropogenic interactions.

As research into the ecological impacts of human activity advances, it is important to clearly define relevant processes. Here, we aim to provide a clear definition of human-commensalism embedded within an ecological and evolutionary framework. This definition should inspire novel research questions regarding the origins of human-commensalism, shared demographic histories of humans and human-commensals, pace of adaptation to anthropogenic landscape modification, and future responses to anthropogenic change.

An ecologically and evolutionarily relevant definition of human-commensalism

We define human-commensalism as a function of dependence on human resources and genetic differentiation from the ancestral, non-commensal population (Box 2). Here, human-commensalism is defined at the population level. Consistent with the ecological definition of commensalism,

Box 2. Visualising human-commensalism in an ecological and evolutionary framework

Human-commensal populations should depend upon anthropogenic resources and be genetically differentiated from the ancestral population (Figure IA). By contrast, 'human-associated' populations span a much broader range within this theoretical continuum (grey gradient in Figure IA), varying in the extent to which they use human resources (e.g., opportunistic scavenging versus systematic exploitation) and how strongly differentiated they are from the non human-associated population. The exact boundaries at which populations can be considered human-associated are not easily definable and are highly context-dependent. Populations which do not interact with anthropogenic resources (e.g., deep-sea marine vertebrates or desert invertebrates with limited range) may be considered non human-associated (dotted region in Figure IA). There may also be a small number of human-associated populations that depend on human resources but are not genetically differentiated from the ancestral population (striped region in Figure IA). As human activity continues to increase, and more populations overlap with anthropogenic environments, future populations may increasingly fall within this region.

Several hypothetical trajectories through this space are possible. Figure IB represents the simplest hypothetical trajectory from no human association to human-commensalism. Over time, a population gains dependence on one or more anthropogenic resources, whilst becoming increasingly genetically differentiated from the ancestral population. An example would be the house sparrow (*Passer domesticus*) (star in Figure I) [36]. Figure IC represents a currently human-associated or synanthropic population that may become human-commensal in the future. Recent anthropogenic activities, including urban expansions, have introduced novel niches which some populations may rapidly adapt to fill. Whilst these synanthropic populations may opportunistically interact with human resources, they are not currently dependent on such resources for persistence. Some synanthropic blackbird (*Turdus merula*) populations (circle in Figure I) may fall on this trajectory [77]. Figure ID shows how a population may lose its human-commensal status following substantial changes in human land use. Whilst the population remains genetically differentiated from the ancestral form, dependence on local human resources may be lost if the old and new anthropogenic niches are sufficiently distinct. Without a dependence on human resources, a population can no longer be considered human-commensal. Rather, the population is in allopatry with the ancestral population. An example is the common weasel (*Mustela nivalis*) in Israel (triangle in Figure I) [63]. These trajectories are illustrative and the situation in nature is likely to be far more complex.

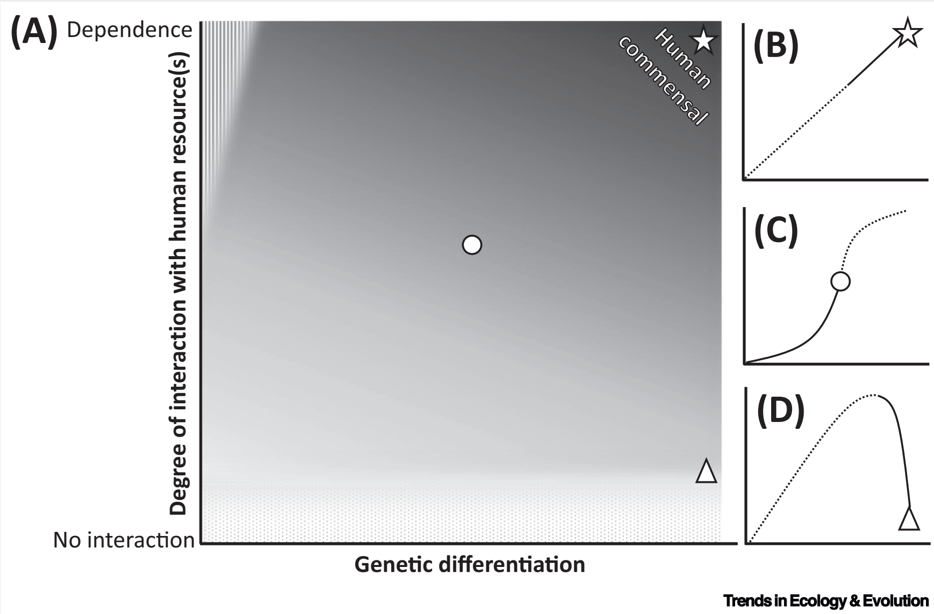

Figure I. Non human association (dotted region) and human association (grey gradient), including the special case of human-commensalism (labelled), represented as a function of the degree of interaction with anthropogenic resources and genetic differentiation from the ancestral population (A). A special case of human association involving dependence on human resources with limited genetic differentiation is also highlighted (striped region). Three hypothetical trajectories through the space are provided (B, C, D) with observed patterns (solid line) and assumed or predicted change (broken line).

Glossary

Adaptation: a process by which individuals become better suited to their environment via genetic change.
Anthropogenic niche: a human-made niche with human-induced modification in resource availability. There can be many, varied forms of anthropogenic niche.
Anthropogenic resource: abiotic and biotic features that are either uniquely available, or found with modified distribution or abundance, within an anthropogenic niche.
Ecological filtering: a series of abiotic and biotic characteristics restrict which phenotypes are able to expand into and colonise a novel environment.
Fitness: the ability of an organism to survive and reproduce in a given environment, passing genetic information to the next generation.
Human-modified environment: a landscape in which resource distribution or abundance is either directly or indirectly manipulated by humans.
Niche constructors: organisms that deliberately or inadvertently alter local environmental conditions, often resulting in the modification of selective pressures acting on themselves or others.
Plasticity: the ability of an organism to express different morphological, physiological or behavioural phenotypes under different environmental conditions.

human-commensalism is associated with approximately +/0 **fitness** effects, wherein the relative fitness benefit incurred by the human-commensal population is larger than any positive or negative fitness effects for the human. Human-commensalism is therefore distinct from other forms of human association (e.g., synanthropy, parasitism) which either do not involve a dependence on human resources or deviate from +/0 fitness effects.

Our definition has many of the same limitations as any definition of complex biological phenomena (e.g., species concepts [44]) and we acknowledge that our discussion may not fully represent all cases of human-commensalism. Notably, we focus on animal taxa as literature describing human-commensal plants is currently limited. However, our definition is applicable to both animals and plants, and we advocate for further research using a wider range of systems. Moreover, we do not consider application of the term ‘human-commensalism’ within the microbial literature. In such contexts, human-commensalism is used to describe all forms of interaction with a human host despite, in many cases, the human fitness effects being non-neutral or unknown [13].

Dependence on human resources

Human-commensal populations should depend upon anthropogenic resources for persistence. Thus, if human resources are removed, these populations should experience extinction or significant declines in population size or range (assessed by researchers in a system-specific manner through observation and demographic modelling). Anthropogenic resource dependence should be multi-generational [45] and distinguishes human-commensal populations from synanthropic populations that only interact opportunistically with human-modified environments [12] (e.g., American black bears, *Ursus americanus*, scavenging urban human food waste [46]).

Anthropogenic resources represent a broad class of biotic and abiotic resources that are either exclusively available or occur with modified distribution or abundance within an **anthropogenic niche**. Examples include sheltering opportunities [47], breeding and overwintering sites [48,49], altered water availability [50], modified soil nutrient compositions [1], and high-quality food supplies that exhibit less seasonal variation than natural sources [47,51]. These anthropogenic resources should exist in an externally constructed niche and arise due to human activities, thus excluding the human body from acting as the resource.

The type and number of anthropogenic resources utilised varies amongst human-commensal populations. Some human-commensal populations specialise on one anthropogenic resource type. For example, barn swallow (*Hirundo rustica*) populations use human-built structures as nesting sites but likely do not directly exploit human food sources [52]. By contrast, some groups, including species colloquially classified as pests, exploit multiple resources. The brown rat (*Rattus norvegicus*) uses landfills, abandoned buildings, and sewerage systems for shelter, and feeds on human refuse [53]. The type and number of resources a population depends upon will impact how that population responds when anthropogenic resources are removed (i.e., with population extinction or merely population decline).

There are many forms of human-modified environment, which have arisen across different timescales (Box 3) [47]. Anthropogenic resource availability varies spatially and temporally depending on the type of environment utilised and the extent of human occupation or maintenance [12]. If humans cease to actively use or maintain an environment, local human-commensal populations will experience extinction or strong population decline. For example, reduced anthropogenic food availability, arising from a sudden reduction in human activity following COVID-19 lockdown restrictions in Singapore, likely led to a >50% reduction in rock pigeon (*Columba livia*) abundance at open food centres [16]. Human-commensal populations should therefore depend upon one or

Box 3. Complexity of the anthropogenic niche

Human-commensal populations depend upon resources found in the 'anthropogenic niche': a human-made niche with human-induced modifications in resource availability [12]. The most obvious contemporary form of human-made niche is the urban environment, characterised by abundant human-made structures and a high concentration of anthropogenic resources. Consequently, human-commensal populations have been well studied in the context of urban ecology [56].

However, human landscape modifications vary in form and intensity. Agricultural landscapes are equally modified by humans, also representing an environment with unnatural fluctuations in resource availability [12]. Even amongst agricultural environments, variation exists. A livestock farm, for example, is likely to provide more consistent food resources across the year than a crop field where harvests lead to annual, rapid depletions in resource availability. In reality, most environments, including those considered 'natural' or 'wild', such as non-fragmented forests or deserts, have undergone some form of human modification [81]. By stipulating that human-commensal populations must live in environments with consistent human habitation or active use in our definition, we acknowledge this variation in human land use modification, whilst restricting the number of systems that can be considered human-commensal, to avoid the term becoming meaningless.

If we more closely consider and compare the type of anthropogenic environments exploited by human-commensals, we may find variation in adaptive responses to human modification. Black rats (*Rattus rattus*) in urban and rural environments, for example, have become specialised on different dietary niches, utilising higher quality, less varied diets with increasing human settlement density [74]. Some human-commensal populations may become so specialised on one form of anthropogenic environment that local transitions in land use detrimentally impact population size. This may explain why some human-commensals traditionally labelled as 'urban exploiters' are now experiencing population declines in the city, but continue to thrive in spatially and temporally distinct rural settlements. The recent population decline of house sparrows (*Passer domesticus*) in both urban and agricultural contexts offers an example of this [82]. More long-term consideration of the history of human land use, beyond what is currently observable, may therefore prove important when considering human-commensal populations in modern environments.

more anthropogenic resources found in environments which are consistently used or maintained by humans.

Genetic differentiation from ancestral, non-commensal populations

Human-commensalism represents an evolutionary adaptation, with adaptive genetic divergence driving phenotypic change. Human-commensal populations should therefore be genetically differentiated from the ancestral, non-commensal population. As adaptation may occur via changes in allele frequency in a single gene or multiple interacting genes, any genetic differentiation that contributes to a divergence in phenotypes associated with human-commensalism is important. In some cases, however, human-commensal and extant non-commensal populations may undergo sufficient differentiation to become reproductively isolated (e.g., the bed bug, *Cimex lectularius* [54]).

When a population expands into a novel anthropogenic niche, early differentiation via genetic drift may occur due to founder effects, as seen during recent urban colonisations by the burrowing owl (*Athene cunicularia*) [55]. Alternatively, the human-modified environment may impose or modify a geographic barrier, leading to allopatric divergence or direct anthropogenic selective pressures, resulting in a genetic bottleneck [56]. Additionally, **ecological filtering** will promote colonisation of human-modified environments by individuals with high levels of behavioural plasticity or ancestral traits that enhance fitness within the anthropogenic niche [57] (e.g., disturbance specialisation in black rats, *Rattus rattus* [27]). For a human-commensal population to emerge, divergent selection should lead to the accumulation of phenotypic adaptations which, combined with ongoing drift, lead to further genetic differentiation from the ancestral population [56]. As anthropogenic resource dependence increases, population-level dispersal will become increasingly coupled with human population movement [22,58]. Associated range expansion or translocation by humans may increase geographic isolation from the ancestral population, further limiting gene flow and potentially accelerating genetic differentiation [59].

The ability to respond to anthropogenic selective pressures is unlikely to be uniform across all populations of a species. Thus, we expect human-commensal status to vary by population. Tree sparrows (*Passer montanus*), for example, closely associate with humans in East Asia but show limited human association in western Europe [60]. Human-commensal status in house mouse (*Mus musculus*) populations is similarly variable, particularly within countries with few natural competitors, such as New Zealand [61]. Within populations, there may also be variation in anthropogenic resource use, for example linked to sex, developmental stage, or seasonality. However, on average, there will be sufficient anthropogenic resource dependence within the population that loss of these resources would lead to population decline. There are a limited number of scenarios in which all populations of a species might be considered human-commensal, such as when all non-commensal populations are outcompeted or go extinct. However, a population-level consideration of human-commensalism is the most generalisable approach.

Origins of human-commensalism

Human activity can directly influence the abundance, availability, distribution, or type of resources available in a habitat, establishing a new anthropogenic niche [4] (Figure 1). The new niche may initially overlap considerably with the ancestral niche. Some individuals, such as those with high behavioural flexibility or alleles well suited to the novel niche, will gain the greatest fitness benefits from exploiting the new resources [62]. Across generations, populations may begin to specialise or become dependent on one or more human resources, particularly if the fitness landscapes separating the ancestral and novel niches generate strong divergent selection. While differentiation may initially reflect divergence at neutral loci, the accumulation of adaptations over time will drive further differentiation from the ancestral niche, reducing gene flow and leading to genetic differentiation from the ancestral population. With increasing dependence on anthropogenic resources, further adaptation will occur, ultimately leading to the formation of human-commensal populations that are dependent on anthropogenic resources and genetically differentiated from the ancestral form. This process may be analogous to the early stages of domestication [30], but the lack of subsequent artificial selection differentiates human-commensals from domesticates.

The origins of human-commensalism are unlikely to be predetermined or follow the same trajectory in all populations (Box 2). Anthropogenic environments are complex and vary spatially and temporally, generating multiple potential pathways to occupation. If resource availability does not differ substantially between the ancestral and anthropogenic niche, it is unlikely that adaptation will occur, establishing human-associated, rather than human-commensal, populations. However, if the novel niche is initially different, or becomes increasingly distinct over time, adaptation will be necessary to ensure population persistence. Human-commensalism can arise only in the latter scenario, as adaptation is required for anthropogenic resource dependence. Subsequent changes in anthropogenic environment (e.g., from a village to an urban centre) may either lead to further adaptation and persistence or population decline and potential extirpation if the human-commensal is unable to transition to the new anthropogenic niche (Figure 1). Ancient common weasel (*Mustela nivalis*) populations, for example, may have been human-commensal in Israel but are now locally extinct, despite ongoing local human habitation [63].

Ecological and evolutionary applications of the definition

A clear definition of human-commensalism, embedded within ecological and evolutionary theory, facilitates consideration of a broader range of research questions. As well as providing insights into our own species' demographic history, human-commensal populations can act as model systems for understanding the pace and form of adaptation to human landscape modification. Consideration of previous adaptive change in human-commensal populations may also enable prediction of future adaptation to anthropogenic activity.

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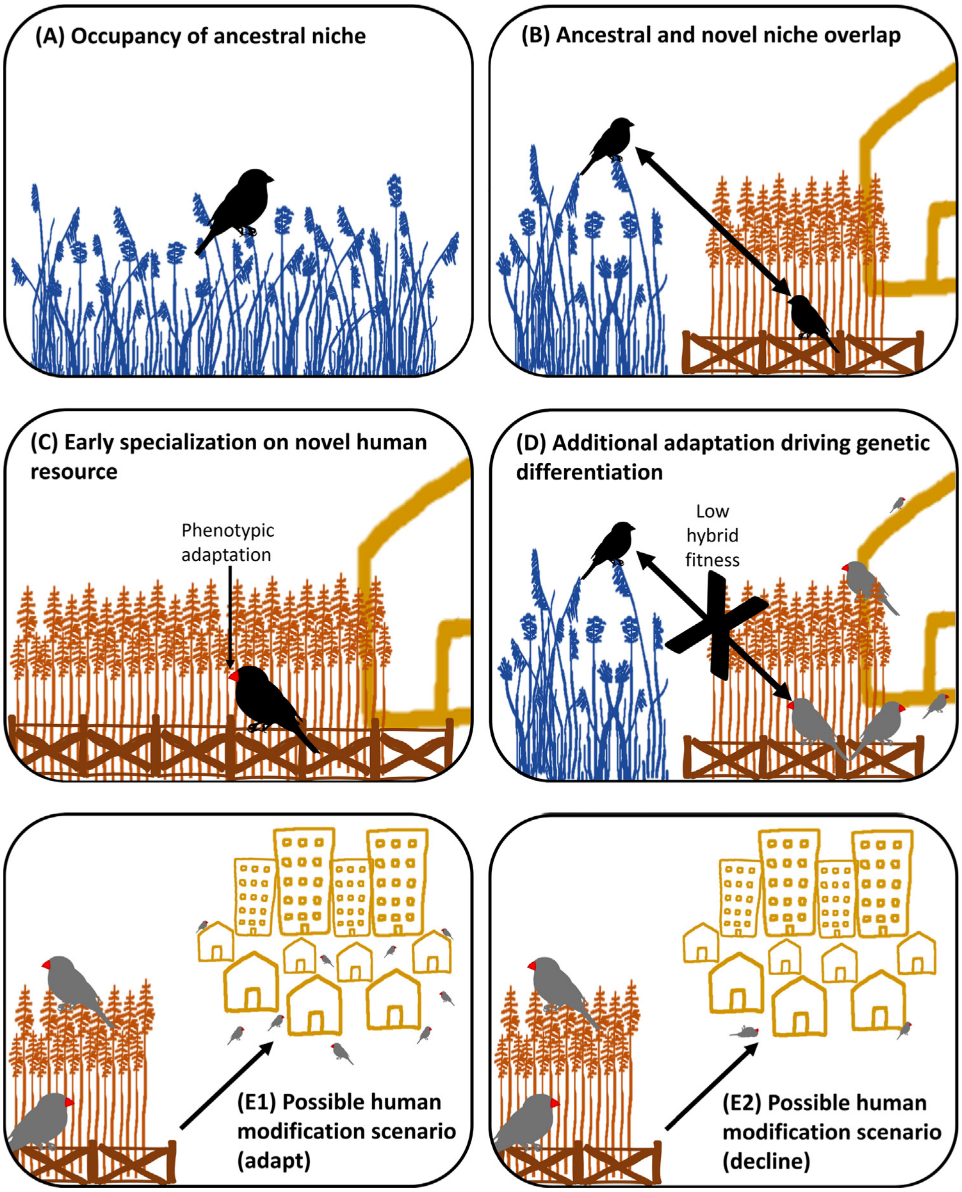

Figure 1. Visual representation of the potential origins of human-commensalism. A population, existing within the ancestral niche (A), experiences novel range expansion into a human-modified environment, such as a small-scale farm. Initially, the human niche is similar enough to the ancestral niche that exploitation can be achieved via phenotypic plasticity (B). Over time, novel pressures within the anthropogenic niche will drive adaptation and specialisation on one or more anthropogenic resources (C). Gene flow with the ancestral population will be reduced, resulting in genetic differentiation. This may result in low hybrid fitness (D). Further modification to the human environment, such as the establishment of a city, could affect the resulting human-commensal population in different ways (E). Some populations may undergo further adaptation and thrive in this new environment (E1). Other populations may prove unable to respond to the change in anthropogenic niche and experience significant population declines or extinction (E2). The two possible human modification scenarios are not mutually exclusive, meaning, for example, that a population that initially undergoes some adaptation to the new environment may experience subsequent population decline or extinction. Note that the panels are presented sequentially here for ease of visualisation. This should not be interpreted to suggest that human-commensalism is a predetermined process or that all populations will follow identical trajectories.

Biogeography and demography

Human-commensal distributions and demography have been shaped by human activity, mirroring the spread of agriculture, trade, and travel networks [1]. The black rat, for example, shares its dispersal history with humans, undergoing two major expansions into temperate Europe during the Roman and Medieval periods [64]. This was likely facilitated by the development of fixed settlements interconnected by terrestrial and marine trading routes. Such tight range coupling means that human-commensals represent ecologically relevant bio-proxies of human demographic history [58]. For example, analysis of mitochondrial DNA phylogenies of the deliberately introduced Pacific rat (*Rattus exulans*) has provided insights into human settlement and dispersal patterns within the Pacific [65]. Furthermore, knowledge of human population movements can be used to understand the spread of many, now globally ubiquitous, human-commensals [20,27,28,66].

Pace of adaptation

Human-commensal populations may act as models for understanding the pace of adaptation to human-modified environments. Recent advances in urban ecology have provided insights into how populations respond to a distinct form of human landscape modification, often emphasising rapid adaptation over short evolutionary timescales [56]. Whilst insights into trait adaptation in contemporary anthropogenic environments are important, it is also necessary to consider the ways in which humans have influenced the evolutionary trajectories of non-human species over extended time periods [67]. During the Late Pleistocene, nomadic hunter-gatherer populations modified landscapes, purposefully manipulating fire and introducing anthropogenic food waste [2,67]. During the Neolithic, the development of agriculture generated more substantial environmental change, introducing novel anthropogenic selective pressures and intensifying existing ones [1]. Exposure to ancient selective pressures may have led to the emergence or maintenance of traits that, through ecological filtering, have facilitated colonisation and enhanced fitness in modern, urban environments [57]. Several human-commensal populations – including house mice [29,68], house sparrows (*Passer domesticus*) [15], and fruit flies (*Drosophila melanogaster*) [69] – have human-commensal origins in the Neolithic. Although small sample sizes may limit our ability to detect genetic differentiation in some zooarchaeological investigations, studies of human-commensal populations could enable consideration of adaptations encompassing longer-term human land use change. We may find a slower pace of adaptation than first assumed, or that population history is punctuated by periods of rapid adaptation followed by relative stasis.

Forms of trait adaptation

Human-commensalism may be associated with a range of phenotypic adaptations. Cognitive and behavioural adaptations including reduced neophobia, aggression and territoriality, enhanced problem-solving abilities, or changes in migratory behaviour have been identified in mammalian and avian human-commensals [36,38,70–72]. In house mice, human-commensalism is associated with reduced aggression levels, potentially because the superabundance of resources in human-modified environments reduces the need for aggressive territoriality and food hoarding [70]. House mice may also illustrate the impact of long-term human association on behavioural adaptation; house mice subspecies with more ancient human-commensal origins perform better in problem-solving tasks [72]. Studies of such behavioural phenotypes could enable consideration of Tinbergen's questions regarding trait function and evolution [73], as applied to human-commensal populations. Furthermore, human-commensalism may be associated with physiological and morphological adaptation. An improved ability to digest starch [36,37,74] or changes in craniofacial morphology [35,36,75] may enable anthropogenic food resource specialisation. Similarly, changes in body size and shape in human-commensal mice may represent adaptations enabling the navigation of complex 3D buildings and human structures [76]. Consideration of the behavioural, physiological, and morphological traits associated with human-commensal populations will facilitate identification of adaptations associated with anthropogenic resource dependence.

Predicting evolution

Evolutionary biologists have long been interested in how populations respond to novel selective pressures to expand into new environments [77]. As the proportion of human-modified land increases [3] so will the number of populations influenced by human activities and the potential for new human-commensal populations to emerge. Comparison of existing human-commensal populations may enable assessment of the consistency in anthropogenic selective pressures across different human-modified environments. Such comparisons could inform predictions of which form of human landscape modification will generate the strongest directional selection for human-commensal evolution, which populations are most likely to become human-commensal, and what traits these populations might possess.

Modelling the order and timescale of trait emergence in human-commensal populations would enable consideration of the repeatability of the evolution of human-commensalism. If the evolution of human-commensalism proves somewhat repeatable, it may be possible to forecast future adaptation to anthropogenic niches in populations currently restricted to opportunistic human resource exploitation. For example, blackbirds (*Turdus merula*), whose recent opportunistic expansion into urban environments has been associated with a partial loss of migratory behaviour [77], represent candidates for future reclassification as human-commensals. Loss of migratory behaviour may be an early behavioural consequence of sufficient resource provisioning in the new anthropogenic environment, facilitating restricted gene flow with ancestral populations, genetic differentiation, and local adaptation. As research moves from understanding past evolution to predicting future evolution [78], an understanding of human-commensal populations could inform predictions of future population-level responses to anthropogenic change.

Concluding remarks

Human-commensalism represents a population-level dependence on anthropogenic resources for persistence, associated with genetic differentiation from the ancestral, non-commensal form. Having a definition tightly coupled with ecological and evolutionary theory means that we can address a broader array of research questions, from considering adaptation to human landscape modification across different timescales to predicting future adaptation in an increasingly human-modified world. Yet, in-depth considerations of human-commensalism raise several questions regarding the ecological conditions required for human-commensal emergence and persistence, particularly when acknowledging that ‘the anthropogenic niche’ is not a homogeneous environment (see Outstanding questions). As humans continue to construct new niches, being able to clearly identify populations that not only interact with human-modified environments, but depend upon them, could facilitate more nuanced assessments of the impacts of anthropogenic activities on biodiversity.

Outstanding questions

How can we usefully define an anthropogenic environment when 95% of the Earth’s terrestrial surface has undergone some form of human landscape modification?

What distinguishes an anthropogenic resource from a natural resource in an increasingly human-modified world?

What is the relative importance of each anthropogenic resource type on the origins and maintenance of human-commensalism? Are certain resources or environments more likely to be exploited by emerging human-commensal populations?

Is there repeatability in the evolution of human-commensalism? Can this be used to speculate on an order of trait emergence during the evolution of a new human-commensal population?

How many generations are needed for anthropogenic resource specialisation and reductions in gene flow? Over what timescale does the evolution of human-commensalism operate?

Why do some human-commensal populations depend on human resources to the extent that they will go extinct if the resources are removed, whilst other populations may still persist, albeit in reduced numbers?

How do transitions in human land use affect human-commensal populations? Will current human-commensal populations survive future anthropogenic change? What traits likely determine whether a population thrives or declines in a modified anthropogenic environment?

Are examples of human-commensal plant populations as common as human-commensal animal populations? Is there an ecological or evolutionary reason one would be more likely to emerge than the other?

Acknowledgements

We thank Marcel E. Visser for contributing to early discussions of this topic and three anonymous reviewers for useful comments on an earlier version of the manuscript. This work was supported by a Research Council of Norway grant (314866) to G.P.S., M.Ra., and M.Ro., and a National Science Foundation grant (1947306) to E.S.

Declaration of interests

The authors declare no competing interests.

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