

Opinion

In the shadows: wildlife behaviour in tree plantations

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Destruction of natural habitats for tree plantations is a major threat to wildlife. These novel environments elicit behavioural changes that can either be detrimental or beneficial to survival and reproduction, with population – and community – level consequences. However, compared with well-documented changes following other forms of habitat modification, we know little about wildlife behavioural responses to tree plantations, and even less about their associated fitness costs. Here, we highlight critical knowledge gaps in understanding the ecological and evolutionary consequences of behavioural shifts caused by tree plantations and discuss how wildlife responses to plantations could be critical in determining which species persist in these highly modified environments.

Impacts of tree plantations on animal behaviour

A primary threat to global biodiversity is the expansion of tree plantations to meet worldwide demands for timber, energy, food, and other tree products [1]. With about a quarter of wildlife currently facing extinction due to human activities [2], there is a growing need to understand how animals are responding to these fast expanding new habitats. In the past decade, research on how tree plantations affect biodiversity, population abundance, and the functional traits of wildlife has increased immensely [3–5], revealing potentially deleterious consequences for many taxa.

Tree plantations are defined as any extensively managed native or exotic arboreal species planted for economic purposes (Box 1). Here, we consider both forestry and certain crops or orchards comprising trees with forest-like structures (hereafter ‘tree crop plantations’), such as oil palm (*Elaeis guineensis*), shade coffee (*Coffea* sp.), and banana (*Musa* sp.), but not grass crops (e.g., wheat, rice). These plantations comprise either a single (monoculture) or several (polyculture) species (Figure 1A). With over 700 000 hectares of natural forest logged annually for forestry [6], plantations are a major cause of deforestation globally. In addition, reforestation and tree planting threatens the biodiversity and ecosystem services of 900 million hectares of grassland, savannah, and open canopy woodlands [7]. Forestry plantations currently occupy ~3% of the world’s forested areas [8], representing ~131 million hectares, with many millions of additional hectares covered by tree crop plantations. Five common tree plantations (Box 1) alone occupy ~112 million hectares of land compared with the ~80 million hectares [9] covered by urban areas.

Despite the increasing landmass covered by tree plantations, we know little about how changes in wildlife behaviour in plantations might contribute to global biodiversity decline. Behavioural adjustments are beneficial when they allow individuals to successfully exploit novel conditions and provide time for selection on standing genetic variation to act and, in so doing, promote local adaptation [10]. However, behavioural shifts can also be maladaptive and lower reproduction and/or survival [11]. Understanding if, and how, animals adjust their behaviour is crucial to predict why some species persist in anthropogenic habitats while others flounder. Yet, we

Highlights

Forestry and tree crop plantations create novel environments that can threaten wildlife by disrupting ecologically relevant behaviours that are essential to their reproduction and survival.

Behavioural shifts in plantations can arise from changes to the environment that affect movement and habitat use, and from more subtle effects, including changes to the sensory environment and/or by altering the physiological state of individuals.

Identifying the underlying mechanisms and fitness consequences of behavioural adjustments by wildlife to living in or near tree plantations is crucial to understand whether and how wildlife adapts to these highly modified environments.

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know surprisingly little about the immediate impact of tree plantations on wildlife behaviour – or their longer-term consequences.

When compared with other highly modified environments, such as cities, tree plantations may appear more akin to the kinds of habitats that animals would naturally encounter, leading to assumptions that any impacts would be reduced. That said, tree plantations and other forms of human-induced habitat modification share many characteristics, such as greater exposure to pollutants, altered predator/prey communities, and habitat fragmentation. Thus, studies of urban ecology may help guide research questions when studying wildlife behaviour in tree plantations. For example, are behavioural traits selected in urban areas similarly selected for in plantations (e.g., neophilia)? Here, we use the existing literature to summarise the main ways in which tree plantations drive changes in wildlife behaviour and highlight key knowledge gaps.

What do we know?

The most widely studied wildlife behavioural responses in tree plantations are those driven by rapid habitat transformation (Figure 1B). Tree plantations often differ structurally to the natural habitats they replace, with either fewer (cf. natural forest) or more (compared with a grassland) arboreal species. Such habitat alterations are often associated with changes in microclimate (e.g., humidity, temperature), abundance and types of prey and predators, and essential resources, including food, nesting, and roosting sites. Another major effect of plantations – although not directly associated with habitat transformation – is human presence. All these alterations can have direct and immediate effects on animal behaviour (Table 1). Unfortunately, we rarely know the unpredictable cascading ecological effects or fitness impacts of these behavioural changes. For instance, increased nocturnality to avoid human activity can lead to novel species interactions that increase competition, thereby altering hunting, foraging, sociality, and

Box 1. Summary of some of the main tree plantations globally

Eucalypt (*Eucalyptus* spp., ~22 Mha), pine (*Pinus* spp., ~54 Mha), rubber (*Hevea brasiliensis*, 7.73 Mha), coffee (*Coffea* sp., 8.2 Mha only in the top ten production countries), and oil palm (*Elaeis guineensis*, ~20 Mha) are among the most globally widespread species used in forestry and tree crop plantations. We use these five species to represent a variety of plantation types, noting also that their main production is in different areas of the world.

Eucalypts (Figure 1A) are the most extensively grown broadleaf tree species. They are planted for pulp extraction and are characterised by the release of allelopathic substances, short rotation periods with associated high disturbance, and strong competition for water that constrains the growth of understorey vegetation. Eucalypts have major detrimental effects on both terrestrial and aquatic wildlife [70].

Pines (Figure 1B) are the most widely planted coniferous trees, mainly grown for pulp and timber. Pines cause acidification of the soil and water and provide strong shading, with often near-complete disappearance of the understorey. Pine plantations are associated with large alterations in species communities and functional diversity [71], and high numbers of pest species [72].

Rubber (Figure 1C) is an increasingly large-scale tree crop plantation in the tropics, especially in Asia. It is planted for its latex that is mainly used in the automobile tyre industry. It is associated with water and soil pollution due to latex extraction, intensive use of pesticides, and soil desiccation. There is biodiversity loss of up to 60% in some taxonomic groups [73].

Coffee (Figure 1D) is a widely distributed tree crop plantation at mid-altitudes in the tropics. When planted as a shade polyculture, coffee plants form part of a forest-like vegetation with canopy trees and a complex structure. Although sun-coffee can have negative effects on wild communities, under appropriate management, shade-coffee polycultures might contribute to wildlife conservation and act as corridors between fragmented forest patches [74].

Oil palm (Figure 1E) is the primary exotic tree crop monoculture in Indonesia and Malaysia, and the most rapidly expanding crop in other tropical areas such as the Amazon. It is used to produce palm oil for food, industry, and biofuel. It is associated with intense logging of natural forests, soil, water, and air pollution, climate change, and the loss of endangered species [75].

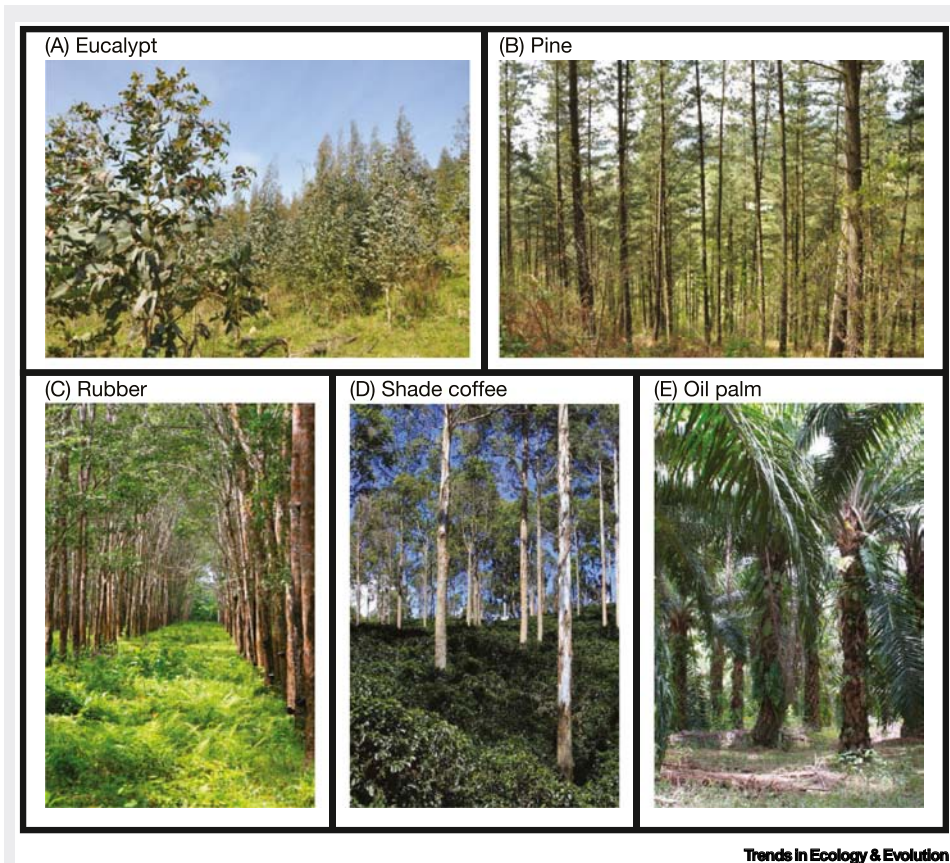


Figure 1. Five of the most common forestry and tree crop plantations. Photo credits: (A) M.I.-C.; (B) M.I.-C.; (C) ‘rubber plantation’ by tobym (CCBY-NC-ND 2.0); (D) ‘Driving through Turialba’ by Ecoagriculture Partners (CCBY-NC-SA 2.0); and (E) ‘Oil palm plantation’ by CIFOR (CCBY-NC-ND 2.0).

antipredatory behaviours [12,13]. Long-term consequences of any behavioural adjustments in tree plantations require a deep exploration of a range of taxa (for examples in primates, see [14]).

The most important consequence of any behavioural shift is, of course, its effect on fitness, since rates of survival and reproduction determine population dynamics and whether a species persists, or even thrives, in tree plantations. Habitat modifications, like tree plantations, can create ecological traps whereby individuals preferentially settle in poor-quality habitats due to misleading cues (e.g., tree plantations might resemble suitable forest habitat to dispersing animals), with consequential declines in fitness [15]. But this is not always true. In cities, for example, adaptive feeding or breeding responses of species that exploit new resources [16,17] have led to similar or even better reproductive performance and longer lifespans than in their natural environments [18]. Whether this is the case in plantations remains unknown as we lack appropriate comparisons of wildlife population dynamics between plantations and natural habitats. Exploring the cues animals use for habitat selection is key to determining whether plantations falsely mimic high-quality habitats, resulting in maladaptive behavioural decisions affecting settlement by dispersing individuals or migrants [15]. In some birds, for example, dominant males prefer to establish territories in plantations rather than in natural habitats, which lowers their reproductive

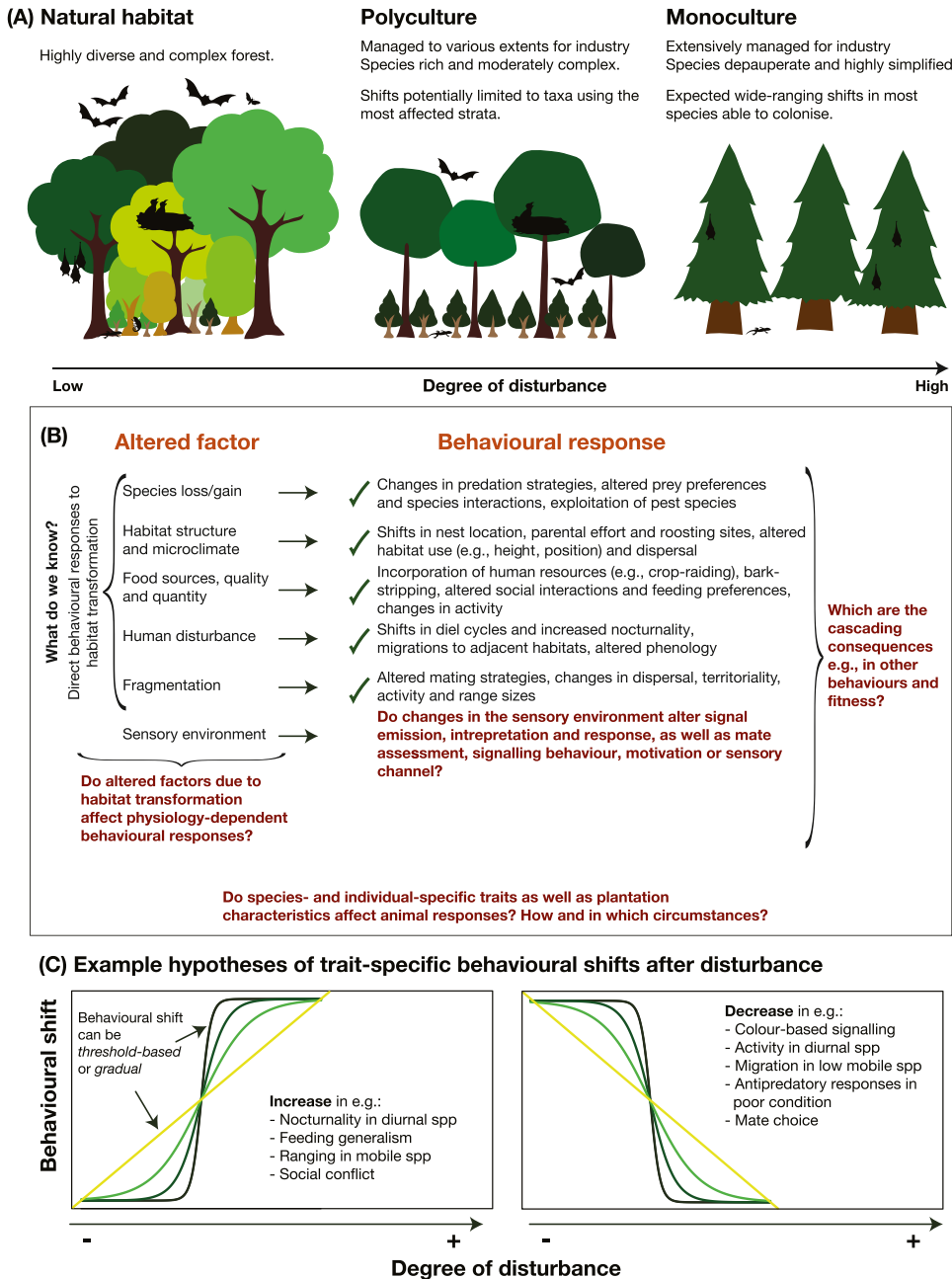


Figure 1. (A) Representation of the structural complexity in plantations and how this could affect ecologically important behaviours. Examples show a hypothetical scenario, highlighting the expected difference in responses between monocultures and polycultures when the natural habitat replaced is a forest. Scenarios where plantations are established in areas covered by more open habitats, such as grasslands or savannahs, will differ since the structure in plantations would include more trees and a closer canopy than in the original habitat. (B) Summary of knowledge gaps, with the main ones highlighted in red and green ticks showing the most common behavioural shifts described in the literature. (C) List of some species and individual-specific traits that can shape the behavioural responses of animals encountering plantations.

Table 1. Examples (from 2010 onwards) of the main behavioural shifts described in the literature in response to three key changes associated with tree plantations: altered structural complexity, altered plant species diversity and animal communities, and increased human disturbance (due to human presence or management activities)^a

Behaviour	Taxa	Effect observed in the tree plantation	Refs
Altered structural complexity, tree species diversity, and animal communities			
Breeding	Bird (<i>Accipiter nisus granti</i>)	Positive breeding and nest survival outcome	[58]
Breeding	Bird (<i>Parus major</i>)	No effect in clutch characteristics, but lower food availability	[82]
Roosting preferences	Bat (<i>Mystacina tuberculata</i>)	Preferred by some individuals; no shifts in roosting behaviour	[83]
Roost use	Bat (<i>Stumira hondurensis</i>)	Used as roosting habitat, with effects on feeding and daily movements	[84]
Activity	Marsupial (<i>Dromiciops gliroides</i>)	Narrower and temporally more restricted activity	[85]
Dispersal and movement	Amphibian (<i>Anaxyrus terrestris</i>)	Microhabitat selection and movement toward avoiding desiccation in dry groundcover caused by plantations	[86]
Colonization ability	Beetles	Presence of an insect larvae promotes the colonization of deadwood by other insects, improving the quality of pine wood	[87]
Habitat use and foraging	Mammal (<i>Prionailurus bengalensis</i>)	Higher activity, habitat use, and effectiveness foraging on exotic rats with increased understorey	[53]
Habitat use and diet	Primate (<i>Macaca nemestrina</i>)	Use of plantations for feeding, and forests for locomotion, resting, and social interactions	[88]
Activity levels and foraging	Primate (<i>Alouatta pigra</i>)	Activity, foraging, and seed dispersal similar to the natural habitat	[89]
Foraging, nesting etc.	Primates (several taxa)	Several responses depending on the primate species, for example, exploitation of plantations as a food resource, nesting habitats, changes in range size etc.	[90]*
Foraging	Bird (<i>Phylloscartes ventralis</i>)	Shifts in the height and angle of prey capture and type of manoeuvre used	[91]
Foraging	Bat (<i>Glossophaga soricina</i>)	Simplified and incomplete diet with unknown consequences	[92]
Foraging	Primate (<i>Macaca nemestrina</i>)	Diet composed of oil palm fruits and pest rats	[54]
Macronutrient preference and food exploitation	Ants (several species)	Less carnivory, and with lower food exploitation rates	[93]
Prey selection	Carnivore mammals (<i>Leopardus guigna</i> , <i>Pseudalopex griseus</i> , <i>Pseudalopex fulvipes</i>)	Altered prey preferences as a consequence of declines in prey availability	[94]
Bark-stripping	Primates (several taxa)	Primates engage in bark-stripping to consume soft bark to compensate for scarcity of natural food	[95]*
Predation of bird nest	Artificial nests	Predation rates dependent on habitat structure (rather than type of forest)	[96]
Predation of pest species	Arthropods and mammals (not specified)	Predation of pest species by native wildlife depends on the type of plantation	[97]
Predation of pest species	Bats (ten European species)	Native bats from different guilds prey upon pest species	[51]
Habitat establishment preference	Bird (<i>Saxicola torquatus</i>)	Not preferred by territorial males, but no differences in fitness between different habitats	[98]
Sociality	Primate (<i>Macaca nemestrina</i>)	Altered positive social interactions, aggression levels, and mother–infant relationships	[99]
Human disturbance			
Activity patterns	Mammals (several species)	Some of the explored species increased nocturnality to avoid human presence	[100]
Use of orchards for foraging	Primates (<i>Pan troglodytes</i>)	Chimpanzee level of overlap with humans and home ranges vary between habitats and are dependent on the cost and benefits of access to food	[101]
Habitat use after harvesting	Marsupial (<i>Phascogale cinereus</i>)	Dispersion from harvested to non-harvested patches	[102]
Habitat use after clear-cutting	Rodents (<i>Oligoryzomys longicaudatus</i> , <i>Abrothrix longipilis</i>)	Movement behaviour and survival after clear-cutting is species dependent	[103]

performance due to greater competition and reduced food availability [19–21]. Changes in behaviours that prioritise the use of poorer quality habitats are also likely to reduce other key fitness components, such as survival. To determine if, and when, tree plantations become ecological traps, multiple fitness components must be simultaneously measured.

What are the knowledge gaps?

Altered behaviours due to disturbance of the sensory environment

Tree plantations can dramatically alter sensory environments and disrupt animal communication. Behavioural responses to altered sensory environments are an important focus of research for urban ecologists [22], but few equivalent studies in plantations exist (but see [23,24]). Animal signals are finely tuned to the environments in which they have evolved, with signal transmission and detection locally adapted via genetic evolution and/or adaptive phenotypic plasticity. For instance, the advertisement calls of satin bowerbirds (*Ptilonorhynchus violaceus*) living in dense or open forests differ in ways that match the prevailing sound transmission qualities [25]. When local adaptation is due to genetic differences, an inevitable consequence is lower signal efficiency in novel habitats [26], leading to selection for either adaptive plastic adjustment or on standing genetic variation for changes in signalling tactics [27].

In plantations, changes in forest structure alter background colouration and sound transmission, while the leachates of exotic trees or pesticides affect the chemosensory environment. Such alterations can disrupt communication and shift signalling behaviours. For example, limited reception of signals and cues can change the interpretation and responses of organisms (e.g., toward predators and mates in newts [28]). In addition, senders can be less motivated to communicate, or must alter the signals they emit to ensure effective transmission. However, it remains unclear whether and when such changes might create a conflict between signal detection and signal reliability – and how this, in turn, might affect receiver behaviours, such as mate choice. Exploring disturbances to animal communication is especially important because of the potential effects on social dynamics and predator–prey interactions. For example, a change in diet or the presence of novel substances can affect the chemical signals emitted [29] and alter both intra- and interspecific interactions in plantations. If signals and/or signalling behaviours fail to keep pace with the rapid transformation of natural habitats into tree plantations then selection against certain signals, such as bright colouration [30], could lead to rapid population decline. One general prediction is that communication by forest or grassland specialists will be more adversely affected than that of habitat generalists, although this will ultimately depend on whether the signal environment of plantations resembles those that species have encountered in their evolutionary history (i.e., the potential for adaptive plastic shifts in signalling) (e.g., [31]). Unfortunately, we lack the data to test for general effects of tree plantations on animal signals or to identify sources of variation in the magnitude of any effects.

Physiologically mediated shifts in behaviour: condition, stress, and pathogens

Habitat changes in tree plantations, including the presence of pollutants, human disturbance, changes in food availability and quality, alterations to microclimate, and new inter- and intraspecific interactions can alter behaviour because these factors affect body condition, stress levels, and pathogen dynamics [32,33]. This is primarily because behavioural responses often depend on the physiological state of individuals (i.e., diet and health). For instance, dispersal [34], risk-

Note to Table 1:

^aNote that effects due to altered structural complexity versus altered plant species diversity and animal communities have been grouped in the table because the exact reason for the behavioural shift is often difficult to disentangle, or because some studies explore both types of changes simultaneously. The effect observed in the plantation is, in most cases, the shift in behaviour compared with that in the closest natural habitat. References with asterisk are reviews comprising several primate examples.

taking [35], and courtship (examples in Box 2) are often body condition dependent. Maladaptive behavioural shifts, or a reduced ability to perform adaptive behaviours, due to being in poorer physical condition, will tend to lower an individual's fitness and, ultimately, reduce population viability. In tadpoles, for example, individuals exposed to leachates of exotic plants are less responsive to predator cues and engage in more risk-prone behaviour [36], potentially due to a greater necessity to keep feeding when in poor condition.

Similarly, behavioural constraints in the ability to respond to novel challenges might arise due to increased stress responses [37]. For instance, toxicants, such as plant leachates, pesticides, and herbicides, can increase oxidative stress and stress hormone levels which can affect foraging, sexual, and antipredator behaviours [38]. In general, the study of stress hormones could provide important insights into wildlife behaviours with conservation implications. For example, in elephants (*Loxodonta africana*), translocated individuals that suffered high chronic stress used less space and had altered habitat preferences, which – surprisingly perhaps – led them to prioritise the use of plantations over natural forests [39]. However, the generality of such findings remains unclear (cf. meta-analysis in urban areas [40]). For instance, tree crop-raiding has been suggested to reduce nutritional stress in some primates, increasing socialising and grooming for groups near tree plantations [14].

Behavioural responses can also influence the health of wildlife in tree plantations by altering their exposure and susceptibility to disease. Urban ecologists have shown that behavioural responses, such as exploitation of human food, can affect pathogen prevalence and dynamics in urban-dwelling wildlife [41], with similar patterns observed in some primates inhabiting tree plantations [42]. Although comparative data for other taxa in plantations is lacking, we expect this to be a widespread phenomenon whenever individuals congregate around limited resources

Box 2. Case study: shifts in reproductive behaviours and mechanisms of sexual selection

Plantations can alter the behaviours associated with a single evolutionary mechanism in several ways that affect individuals and populations. The direct relationship between sexual selection and individual fitness means that any shift in behaviours associated with male–male competition and female mate choice can have drastic consequences for population dynamics. There are at least four ways in which disturbances due to tree plantations could affect sexual selection.

- (i) Resource quality and access. Lower food quality and reduced abundance, as well as toxins from novel leachates, could constrain the resources and energy invested in the development of costly secondary sexual traits and reduce the time individuals spend on behaviours like courtship and mate choice [33,76]. For instance, exposure to the toxic leachates of eucalypt plantations (*Eucalyptus globulus*) reduced investment into male secondary sexual traits and altered female mating preferences in the European palmate newt (*Lissotriton helveticus*).
- (ii) Sensory environment and animal communication. Variation in the forest structure and microclimatic conditions, in addition to a novel leaf litter, can alter the acoustic, visual, and chemical sensory environments in which the sexes interact. Changes in the sensory environment can affect the reliability of a signal as a marker of quality and the behaviours of the signaller; in addition, environmental changes can reduce the ability of the receiver to detect signals. This can have important population-level consequences if individuals then make mating decisions that lead to lower quality or fewer offspring [77]. Individuals in tree plantations might then face selection to reduce the relative importance they place on the most adversely affected sensory modality to other, less affected, modalities [78].
- (iii) Microclimate. Altered microclimatic conditions resulting from the substitution of natural habitats with tree plantations [79] can lower individual fertility [80]. Since some environmental conditions influence, for example, sperm competitiveness, animals are expected to alter their mating strategies to compensate, via plastic responses or via selection on genetic variation.
- (iv) Population demography. In the agile antechinus (*Antechinus agilis*), reduced population size combined with limited dispersal ability due to highly fragmented landscapes in exotic pine plantations (*Pinus radiata*) altered social interactions, most notably lowering the ability of females to deploy mating behaviours that lead to inbreeding avoidance and reducing the opportunity for sexual interactions with multiple mates (i.e., less multiple paternity) [81].

at higher densities, or when there is less dispersal between plantations due to habitat fragmentation. These conditions alter encounter rates between conspecifics that should affect the transmission dynamics and prevalence of pathogens [43,44], with flow on effects on host behaviour.

In [Box 2](#), we provide a specific case study on sexual selection to illustrate the complexity of both direct and (more subtle) indirect effects that tree plantations might have on the behaviour of individuals and the population-level consequences.

When and why are behavioural responses advantageous?

Trait-specific responses

While plantations lead to the disappearance of some species, others flourish by seizing on novel opportunities through behavioural adjustments (see examples as response to novel environments [11,45]), so exploring how species traits moderate the potential for adaptive behavioural shifts that allow them to exploit tree plantations is essential. An example of animals flourishing in plantations is seen in many pests [46]. Pest species can be either exotic or native [47] and are often adept at altering their feeding behaviour to take advantage of reduced competition and increased food availability [48,49]. Feeding shifts and other behavioural changes can lead to dramatic increases in pest population size and cascading effects on the behaviour of other species. Pest outbreaks can be negative if they increase competition [50], or positive if they provide a novel resource for other species to exploit [51]. For example, in South-East Asian oil palm plantations, native barn owls (*Tyto alba*), leopard cats (*Prionailurus bengalensis*), and pig-tailed macaques (*Macaca nemestrina*) adjust their predatory behaviour to exploit the high densities of exotic rats (*Rattus* sp. [52–54]). The ability to shift feeding habits to exploit novel resources is likely to be more common in species and individuals with high exploratory ability and generalist habits [55].

Apart from capitalising on greater abundance of certain prey, native animals can modify their behaviour to exploit novel niches and resources in tree plantations. Carnaby's cockatoos (*Calyptorhynchus latirostris*), for example, have shifted their foraging in plantations to exploit pinecones, which are now an essential source of food for this endangered bird [56]. Tree plantations can also expand suitable breeding habitat with beneficial demographic effects, as in some raptors [57,58]. The fitness payoffs that wildlife obtain from tree plantations depend on the benefits they seek – and any costs that are thereby incurred. Importantly, these costs and benefits can vary tremendously depending on the type of behaviour and when activities are undertaken (e.g., briefly entering a tree plantation to capitalise on food abundance versus predation risk at that time of day). To determine whether tree plantations benefit native species, we need to measure a wide range of behavioural traits that affect fitness and account for temporal variation in the cost–benefit ratio.

The type and extent of behavioural shifts and the fitness consequences depend on species- and individual-level traits ([Figure 1C](#)). For example, many species show sex-biased long-range dispersal [59], where only one sex leaves the natal group. The effects of any behavioural responses will therefore depend on whether movement into a plantation is temporary or reflects permanent dispersal. The cockatoo and raptor examples noted earlier involve highly mobile species that can readily exploit tree plantations when the net benefits are high, but avoid them to reduce costs incurred at other times of the day (e.g., [60]). Tree plantations could impose a stronger threat to species with low mobility. For such species, adaptive behavioural responses that allow animals to persist are expected to be far more important. Strikingly, there are very few studies in plantations on taxa with low mobility, such as amphibians, reptiles, small mammals, and many invertebrates. We also do not yet understand how low dispersal capacity that can trap individuals in tree

plantations might affect geographic divergence of traits, such as behaviours involved in sexual selection and species recognition [61]. We predict that in the long term, geographic variation in traits and signalling could even promote assortative mating among populations in different tree plantations, although this topic has barely been considered in the plantations literature.

An additional complication: not all plantations are alike

The magnitude of behavioural shifts in response to habitat change will depend on a myriad of plantation characteristics that need to be considered when designing studies, including their structural complexity, geographic region, and size. For example, the more complex forest structure associated with polycultures provides niches and resources for a wider range of species than that of monocultures, helping to maintain diverse predator–prey communities [62], improving ecosystem stability, and reducing pest species outbreaks [48]. Species generally respond strongly to changes in their preferred microhabitat; hence, the simplified structure in monocultures will probably have stronger effects on arboreal than ground-dwelling forest wildlife. Of course, which species exploit plantations will depend on the original pool of species in the replaced natural habitat [63]. Therefore, whether selection favours altered behaviours will depend on the type of natural habitat plantations are replacing (and, hence, the evolutionary history of these species).

Importantly, plantations change over time, and their age and the type of management affect their structural complexity. For example, many crop and pulp plantations are not pruned or thinned, which creates a very simplified understorey due to the lack of light. By contrast, thinning of forestry plantations create an open and diverse understorey. These differences can strongly affect how ground-dwelling species respond. Similarly, younger plantations resemble grasslands or scrublands, while older plantations have a forest-like structure (e.g., see [63]). This suggests not only that species behavioural responses will vary with the age of a plantation, but that species assemblages could also change. Likewise, clear-cuts of forestry plantations may force animals to make rapid behavioural adjustments (e.g., migrate, shift nesting locations [64]), while continuous harvesting of tree crops could lead to behavioural shifts in response to constant human presence.

The magnitude of the effect of plantations on wildlife will vary geographically and depend on the history of plantations. Since exotic plantations impose greater challenges than native plantations for wildlife (e.g., through novel stressors), species in highly biodiverse tropical areas, such as those in South America and Africa, where 97% and 70%, respectively, of all plantations comprise exotic species [8], are most likely to be impacted by plantations. By contrast, in temperate areas, plantations are often monocultures of native trees (e.g., North America and parts of Asia [8]). It might, however, be difficult to tease apart the effects of the origin of the planted tree species from that of the alteration in structural complexity, at least when plantations replace native forests. In temperate zones, forests are simpler, less diverse, long established, and more like plantations than those in tropical areas. Wildlife in temperate areas might therefore be better adapted to the structural characteristics of tree plantations, with less need to modify their behaviour. A testable prediction is that animal behaviours in formerly forested areas (where plantations have been long established) differ from those in recently planted areas or when plantations replace complex natural habitats. This could be due to multiple causes, including differential survival of individuals, strong recent selection on genetic variation, and inbreeding. Although some animals temporarily shift their behaviour and persist in plantations (Table 1), adaptation requires responses that maintain or increase fitness in the long term. We suggest that more research comparing behavioural shifts and their fitness consequences in new and long-established plantations, and temperate versus tropical areas, could shed light on which behavioural modifications permit prolonged persistence.

Landscape-level effects, such as the extent of plantations and their closeness to remnants of original habitat, can also shape behavioural responses. While some plantations replace large areas of native habitat making their inhabitants spatially isolated, others form part of a matrix dominated by natural habitat where animals can make occasional forays into plantations. Landscapes comprising a mosaic of plantations and natural habitats are known to sustain higher diversity of species and healthier communities [65]. But we do not yet know the role of behaviour in the maintenance of such communities. Behavioural plasticity is expected to allow animals to exploit novel resources, allowing for short-term survival when conditions in plantations are beneficial. However, some regulatory plastic behavioural responses can weaken selection and hamper evolution [66], posing a longer-term threat if the natural habitat becomes increasingly rare. An interesting possibility, therefore, is that matrix landscapes are a trap for some taxa if the tree composition of the habitats suddenly changes and they are poorly adapted to plantations.

Wildlife behaviour: conservation and socioeconomic implications

Tree plantations are geared toward improving life for humans and/or maximise economic output, but this usually comes at the expense of wildlife. Understanding wildlife behavioural responses can, however, help reduce the loss of biodiversity and provide better solutions for conservation management [67]. This knowledge is especially important in tropical areas where high rates of deforestation threaten the equally high natural level of biodiversity.

Tree plantations can be considered part of a socio-ecological system, where wildlife behaviour is a primary indicator of healthy ecosystem function. For instance, although monocultures are often presented as a better economic choice than polycultures, behavioural shifts of animals in plantations raise questions about the net socioeconomic benefit. The simplified structure of monocultures, and the consequent reduction in food sources for wildlife, could have weighty economic consequences if predators shift their behaviour to prey on livestock living in or near plantations, or if monocultures promote crop-raiding by herbivores [14]. Human–wildlife conflict is predicted to be lower in more diverse plantations that sustain more complex trophic interactions and a wider range of food sources. Understanding the feeding behaviour of animals in different types of plantations could provide companies with vital insights into plantation design that create a compromise between the needs of humans and wildlife [54]. In addition, monocultures are more prone than polycultures to outbreaks of pest species who have modified their behaviour to exploit novel resources, especially if their predators are locally rare or extinct. It may be possible to reduce the multi-billion dollar annual investment in pest control (e.g., pesticides) by maintaining a greater diversity of tree species and ages to create larger predator communities in plantations [68].

Finally, plantations might even contribute to the conservation of some native and endangered species by providing corridors between preferred natural habitats, and by buffering edge effects, especially when planted on previously cleared land, or when mixed with native trees (e.g., [69]). Improved understanding of the behaviour of wildlife in tree plantations is a powerful way to promote coexistence with local farmers and drive management changes by timber companies. Here, there is great value in carrying out long-term studies that quantify the difference between the perceived and actual socioeconomic value of different tree plantations and the efficacy of management practices, to promote the conservation of wildlife.

Concluding remarks

Understanding if, and how, animals shift their behaviour in tree plantations to enhance their survival or breeding success is essential to develop management strategies that promote the coexistence of wildlife with human economic goals. An important aim should be to design plantations

Outstanding questions

How similar are the behavioural responses in tree plantations to those seen in other human-made habitats, such as those created by urbanisation and other forms of agriculture?

Are there behavioural traits that are consistently beneficial or detrimental during the colonization of different types of anthropogenic habitats (i.e., plantation vs. non-plantation) and does selection against certain behaviours lead to ‘homogenization of wild-life behaviour’?

Are evolutionary responses to changes in the sensory environment rapid enough to allow species to adjust their signals and allied behaviours to the novel environment? Does disruption of communication when deploying the most commonly used mode of transmission select for a switch to alternative communication modalities in tree plantations?

How readily can we extrapolate the behavioural responses observed in one type of tree plantation to those in another? In addition, are responses for a given species similar in monocultures and polycultures, or for forestry and crop plantations, or in different areas of the world? Is it the same if a plantation replaces a forest compared with other types of habitats such as grasslands or open woodland?

Do plantations in tropical areas have stronger effects in inducing changes in animal behaviour that lower their fitness? If so, is this driven by a stronger reduction in structural complexity (when the replaced natural habitat is a forest), by the origin of the planted tree species (exotic vs. native) or both?

How do behavioural responses and selection pressures differ between large-scale plantations and small-scale plantations established within a matrix of native habitats?

Do tree plantations drive divergence of morphological and behavioural traits that might promote reproductive isolation of populations akin to those being reported for urbanization?

that take advantage of behavioural adjustments by wildlife to balance better outcomes for wildlife with fulfilling economic goals. Today, our understanding of the relative importance of how the novel environments created by tree plantations affect wildlife behaviour is limited to a handful of taxa. Many basic questions remain unanswered (see [Outstanding questions](#)). To conserve biodiversity, we need to better anticipate wildlife responses, and their fitness consequences, to the ever-increasing transformation of natural habitats into tree plantations.

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Declaration of interests

No interests are declared.

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What behavioural responses lead to plantations becoming ecological traps versus responses that are adaptive? Are these differences associated with specific biological or taxonomic traits that we can predict (e.g., as has been done in urban ecology studies)?

How do phenotypic traits, such as sex, personality, or age, shape behavioural responses to being in plantations? Are individual responses plantation specific? And what are the long-term consequences for population viability?

What are the main wildlife behaviours that will help us assess the quality of the habitat in plantations as part of a socio-ecological model that promotes human economic goals while simultaneously conserving wildlife?

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