Please cite the Published Version

Shutt, Jack D and Lees, Alexander C (2021) Killing with kindness: Does widespread generalised provisioning of wildlife help or hinder biodiversity conservation efforts? Biological Conservation, 261. ISSN 0006-3207

DOI: https://doi.org/10.1016/j.biocon.2021.109295

Publisher: Elsevier BV

Version: Accepted Version

Killing with kindness: does widespread generalised provisioning of wildlife help or hinder biodiversity conservation efforts?

Keywords: Bird feeding, competition, hyperpredation, supplementary resources, human-wildlife interaction, biotic homogenisation

Abstract

Provisioning of wildlife with food, water and breeding sites is a globally ubiquitous phenomenon. While some provisioning is targeted at single species of conservation concern, generalised provisioning is more common and can exceed the local availability of natural resources for recipient taxa. Generalised provisioning is enthusiastically promoted by many conservation organisations as a means to foster connection with nature and help wildlife. However, such a vast input of additional resources into the environment must have diverse, ecosystem-wide consequences. Direct effects upon recipient taxa have garnered most research interest, and are generally positive in leading to increased survival, productivity and hence population growth. However, we argue that the wider implications for the recipients' non-provisioned competitors, prey and predators are underappreciated and have the potential to generate pervasive negative impacts for biodiversity. The impact of provisioning has also hitherto been considered predominantly in urban contexts, overlooking the movements of wildlife to and from provisioning sources and the widespread nature of both human settlements and provisioning, underappreciating the potential scale of impact. Using a case study of UK garden bird food and nestbox provisioning, we hypothesise how well-intentioned provisioning could be contributing to widespread ecological community change and homogenisation. This may consequently help drive declines in species of conservation concern by asymmetrically benefitting common and adaptable species, leaving their competitors exposed to enhanced direct competition, hyperpredation, mesopredator release and heightened disease transmission risks. We recommend further research into these ecosystem cascades and a more cautious, evidence-based approach to the encouragement of provisioning wildlife.

1. Introduction

Intentional human provisioning of wildlife with food, water, shelter and nesting sites occurs worldwide and constitutes a growing, multi-billion-dollar industry especially prevalent in western culture (Cox and Gaston, 2018; Jones and Reynolds, 2008). Provisioning takes many forms and targets almost every major taxonomic group, from bee hotels (MacIvor and Packer, 2015) through vulture restaurants (Cortés-Avizanda et al., 2016) and shark baiting for tourists (Burgin and Hardiman, 2015; Maljković and Côté, 2011), to waterhole creation for large mammals in arid regions (Landman et al., 2012; Tshipa et al., 2017). While types of provisioning are numerous and diverse and have generally been treated disparately, they all share unifying features and are components of the same socioecological phenomenon.

We believe that the varying types of provisioning can be grouped into four discrete categories along two axes of divergence: (i) targeted provisioning to benefit a specific taxon, or generalised provisioning, and (ii) providing replacement resources, or additional resources (Table 1). The motivations for wildlife provisioning are diverse and differ by provisioning category (Table 1), but are primarily well-intentioned (Brock et al., 2017; Cox and Gaston, 2018). Although there is some disagreement (Baverstock et al., 2019; Jones, 2018), provisioning is often regarded by both the public and conservationists as beneficial for biodiversity conservation (Davies et al., 2012; Jones, 2011; Jones and Reynolds, 2008).

Generalised provisioning of additional resources is the most widespread form and its scale enormous. For example, supplementary feeding of garden wildlife is the commonest active human-wildlife interaction globally, being undertaken by more than half of all households in many western countries (Davies et al., 2012; Jones and Reynolds, 2008). The global birdfood market alone is valued at $5-6 billion and growing by 4% annually (Jones, 2018). In the UK the amount of birdfood supplied in gardens is sufficient to maintain treble the entire combined populations of the commonest feeder-using species if they consumed nothing else (Davies et al., 2009; Orros and Fellowes, 2015) (for further discussion see section 4). Many non-target mammal taxa, including rats *Rattus* sp. and squirrels (Sciuridae), also consume these resources incidentally, but at very high frequencies (Hanmer et al., 2018; Reed and Bonter, 2018), while other more ‘desirable’ mammal species, including hedgehogs *Erinaceus europaeus* in the UK and chipmunks *Tamias* sp. in the USA, are intentionally supplied with bespoke foodstuffs (Cox and Gaston, 2018). Artificial wildlife homes are also provisioned in the millions in gardens for a variety of taxa including mammals, birds and insects (Davies et al., 2009; MacIvor and Packer, 2015).

The massive scale of this resource input likely has significant ecosystem impacts (Jones, 2018; Jones and Reynolds, 2008), and while direct effects on provisioned taxa have garnered some research interest, we contend that the indirect implications are poorly understood. Despite this knowledge gap, wildlife provisioning is actively encouraged by many conservation organisations in many, but not all, countries (Baverstock et al., 2019; Hanmer et al., 2017; Jones, 2011), including the National Wildlife Federation in the USA and the Royal Society for the Protection of Birds (RSPB) in the UK. Herein, we review documented impacts of wildlife provisioning alongside proposing hitherto overlooked and understudied ecosystem cascades to ascertain whether these activities help or hinder biodiversity conservation efforts. We focus on examples involving generalised provisioning of additional resources (Table 1) as this is the commonest, most impactful and least regulated form, but across provisioning forms we would expect similar ecological interactions to be occurring on varying scales.

2. Known direct impacts of wildlife provisioning

2.1. Positive direct impacts

Research into the direct benefits and costs of provisioning upon recipient individuals and species constitutes the majority of work into wildlife provisioning to date. The fitness of food-provisioned individuals often increases, with increased productivity and offspring survival rates (González et al., 2006; Robb et al., 2008b), reduced likelihood of starvation and health complications (Chamberlain et al., 2009; Knutie, 2020; Wilcoxen et al., 2015), enhanced immune function (Strandin et al., 2018) and increased survivorship (Murray et al., 2016; Norris, 1993). Provisioned nestboxes lift limitations from the restricted availability of natural breeding sites (MacIvor and Packer, 2015; Mänd et al., 2009), increase population densities and can raise breeding success (East and Perrins, 1987). Populations of many species provisioned with food or nestboxes have therefore increased at local and regional scales (Mänd et al., 2009; Plummer et al., 2019) (Table 2). Food and water provisioning is particularly beneficial in nutritionally limited, drought susceptible or energetically costly environments (Robb et al., 2008a; Tshipa et al., 2017). This can even lead to loss or alteration of migratory behaviour by allowing individuals to persist in regions year-round that were previously seasonally uninhabitable (Greig et al., 2017; Páez et al., 2018; Plummer et al., 2015; Satterfield et al., 2018).

Resource provisioning, particularly targeted provisioning of both replacement and additional resources (Table 1), has become an important conservation intervention. For example, nest box provision for species occupying degraded forests containing few natural cavities has enhanced conservation prospects for threatened species (Garnett et al., 1999; Olaciregui et al., 2020).

Replacement feeding for vultures which have lost natural resources due to human activity, and to steer them away from contaminated food, is also allowing threatened populations to persist (Cortés-Avizanda et al., 2016). Additional feeding of several threatened species under population management programs has allowed them to expand and/or recolonise former ranges, conferring greater resistance to stochastic events (Clout et al., 2002; González et al., 2006), as has nestbox provision (Carstens et al., 2019). Reintroductions of species of conservation concern often rely on initial additional resource provisioning to encourage population persistence (Cortés-Avizanda et al., 2016; Piper et al., 1999). Indeed, targeted provisioning actions have been among a portfolio of interventions that have saved species including pink pigeon *Nesoenas mayeri,* California condor *Gymnogyps californianus* and orange-bellied parrot *Neophema chrysogaster* from extinction (Bolam et al., 2020). We are however unaware of any species saved from extinction through generalised provisioning.

Provisioning wildlife has also been shown to have important and positive consequences for the provisioner (Table 2). It has been described as a vital link to nature in an increasingly urbanised and nature-disconnected world (Brock et al., 2017; Jones, 2018). Provisioners show greater environmental awareness than non-provisioners and report increased feelings of connection to nature (Cox and Gaston, 2016; Davies et al., 2012) which may foster pro-environmental behaviours in other aspects of life (Cox and Gaston, 2016). Provisioners report being more relaxed due to their engagement with nature and benefit from improved wellbeing and mental health (Cox and Gaston, 2016), while citizen science bird feeding schemes also gather useful scientific data (Jones and Reynolds, 2008).

2.2. Negative direct impacts

In addition to the direct positive impacts of resource provisioning upon recipients, some direct negative consequences are also documented (Table 2). Increased intraspecific disease transmission is associated with large and persistent aggregations around provisioned food sources (Hochachka and Dhondt, 2000; Lawson et al., 2018; Moyers et al., 2018). Generalised provisioning encourages novel interspecific associations which facilitates novel interspecific disease crossovers, which have already driven large declines in some species (Lawson et al., 2018, 2014; Robinson et al., 2010). Diseases can also spread from provisioned wildlife to provisioning humans (Lawson et al., 2014). Elevated wildlife mortality rates around provisioned food may occur (Pavisse et al., 2019; Swallow et al., 2019), with predation by domestic pets as well as window collisions exacerbated by encouraging wildlife into the vicinity of human settlements (Kummer and Bayne, 2015; Pavisse et al., 2019). The reproductive success of recipients might also be negatively affected if they become dependent upon provisioned food resources of poor nutritive value (Chamberlain et al., 2009; Plummer et al., 2013), which can affect blood chemistry (Ishigame et al., 2006; Støstad et al., 2019) with unknown health impacts. Nestboxes can be associated with an increased bacterial load and egg mortality compared to natural cavities (Devaynes et al., 2018), owing to different internal microclimates.

Provisioned resources of all types are often monopolised by dominant individuals and species, resulting in the exclusion of others from local assemblages (East and Perrins, 1987; Francis et al., 2018; Maljković and Côté, 2011; Parsons et al., 2006) (Table 2). Monopolising species are typically abundant generalists well adapted to anthropogenic environments, and often include alien species for which provisioning can aid invasion (Galbraith et al., 2017a, 2015; Le Louarn et al., 2016; MacIvor and Packer, 2015). As invasive species are one of the most significant causes of extinctions globally (Bolam et al., 2020) this may be of significant concern. Habitat damage can also occur when resource provisioning enables persistent gatherings or ecologically unsustainable populations of recipient species to persist (Cooper et al., 2006; Landman et al., 2012). Pollination services can even be reduced due to distraction by provisioned foodstuffs, which may impact vegetation (du Plessis et al., 2021; Páez et al., 2018). A subtle negative impact is that food provisioning can lead to biased offspring sex ratios, a particular problem for Critically Endangered populations (Clout et al., 2002).

3. Our contention – indirect impacts may be far more pervasive than currently appreciated

Research into the effects of wildlife provisioning has tended to focus on provisioned species, neglecting sympatric non-provisioned species. We contend that this bias overlooks trophic cascades, as providing one organism with additional resources impacts all other organisms connected to it in the food web; be they predators, prey, pathogens, parasites or competitors, if these exist in the ecosystem. These interactions may then promote negative ecosystem impacts on biodiversity that have hitherto received scant attention (Table 2).

Increasing populations of provisioned species will provide greater prey abundance for their natural predators and may facilitate an increase in predator populations (Courchamp et al., 2000; Pintor and Byers, 2015; Roemer et al., 2001). As most predators are generalists, increased predator populations supported by artificially inflated populations of provisioned prey species may result in hyperpredation on non-provisioned prey species (Courchamp et al., 2000; Lees and Bell, 2008; Maeda et al., 2019). This could cause declines in the latter, particularly if the non-provisioned prey species exist at low densities (Lurgi et al., 2018; Roemer et al., 2001) (Fig 1, Table 2). Equally, predation by inflated populations of provisioned species may directly hyperpredate their own natural prey resources (Orros et al., 2015; Orros and Fellowes, 2012) (Fig 1).

Hyperpredation of non-provisioned species may be further exacerbated by mesopredator release, following the (often unintended) provisioning of members of this guild, such as corvids, gulls, foxes and rodents (Chamberlain et al., 2009; Hanmer et al., 2017; Reed and Bonter, 2018). While mesopredator release is usually considered in the context of the removal of regulatory apex predators, the opportunistic use of provisioning by this guild may additionally boost their populations (Coates et al., 2020; Hanmer et al., 2017). Mesopredators are common predators of bird eggs and chicks and young mammals and their population increases due to human activities have been linked to declines in many species globally (Coates et al., 2020; Hanmer et al., 2017), reducing biodiversity (Oro et al., 2013) (Fig 1).

A potentially pervasive threat to biodiversity caused by provisioning is increased competition for natural resources between inflated populations of provisioned species and their non-provisioned competitor species (Jones, 2018; Shutt et al., 2021) (Fig 1). Co-occurring species within assemblages compete with each other for limited natural resources but coexist by exploiting subtly different niches and employing varying life-history strategies, each with associated costs and benefits. Provisioning may reduce or eliminate advantages from alternative life history strategies occupied by non-provisioned species, reducing the ability of these species to compete and coexist, for example by reducing the benefits of migration by providing permanent and static artificial resources (Greig et al., 2017; Plummer et al., 2015). Provisioned species could then outcompete competitors for natural resources due to the advantages gained from provisioning (Francis et al., 2018; Galbraith et al., 2015), reducing the number of ecological niches available and hence impoverishing community biodiversity (for specific examples to illustrate these abstract points please refer to section 4). This may be particularly impactful in small forest fragments where threatened species are increasingly being provisioned to allow tourists to view them (Woods et al., 2010), but where competition impacts are probably very important in structuring communities.

Community takeover by dominant species due to human food provisioning is well documented in Australia where boisterous despotic competitor species such as noisy miner *Manorina melanocephala* monopolise supplemental resources, enabling them to actively and aggressively exclude other species (Jones, 2018; Parsons et al., 2006). Equally, in New Zealand, supplementary bird food provisioning disproportionately benefits alien invasive species which consequently further outcompete and replace native species (Galbraith et al., 2017a, 2015). Conservation organisations in both countries are subsequently anti-provisioning, in contrast to general international attitudes (Baverstock et al., 2019). Such impacts of competition may be less overt in other regions, but they will inevitably exist if some species are provided with additional (and often comparatively unlimited) resources not available to their natural competitors (Francis et al., 2018).

Community assemblage changes due to provisioning have been demonstrated (Fuller et al., 2008; Galbraith et al., 2015; Plummer et al., 2019), although these exclusively consider urban ecosystems. These studies have demonstrated supplementary feeding attracting novel species and restructuring the community towards a predominance of feeder-using species (Fig S1), or nestbox-using species (MacIvor and Packer, 2015). While important, this urban focus ignores the large movements and migrations of animals to and from provisioning sources (Greig et al., 2017; Milligan et al., 2017), the widespread nature of human settlements and provisioning (Hanmer et al., 2017), higher provisioning rates often occurring in rural communities (Davies et al., 2012), and that nature reserve management frequently includes provisioning to enhance visitor experience (Woods et al., 2010). Effects are therefore likely to occur across a far wider spatial extent than currently appreciated (Shutt et al., 2021), favouring novel provision-using community assemblages across large areas (Galbraith et al., 2015). As provisioned species are often abundant, adaptable and widespread, similar species benefit ubiquitously across wide geographic areas, and different types of provisioning may benefit the same species’ and exacerbate net impacts, this may contribute to the homogenisation of ecological communities (Newbold et al., 2019; Oro et al., 2013), reducing beta and gamma diversity, even if local alpha diversity increases (Fig S1).

Lastly, the ecological footprint of provisioning must be considered as an indirect impact. Carbon and land use costs in creating and transporting provisioned food are large (Lin, 2005). Land supporting agriculture and forestry used for provisioning replaces land that could be used for human agriculture and forestry, which may drive further habitat loss. As some provisions are produced in tropical countries (e.g. Niger seed (Lin, 2005)) the biodiversity costs of crop growth in more biodiverse regions could outweigh any benefits bestowed upon recipient species in less biodiverse areas where provisioning is conducted.

Combined, and with the massive scale of provisioning, we consider that these indirect impacts could potentially be playing a significant role in ecological community changes, contributing to biotic homogenisation and even local extinctions (Newbold et al., 2019; Oro et al., 2013).

4. Case study: UK garden bird provisioning

Over 17 million UK households (64%) (Davies et al., 2012) spend a combined £250 million on more than 150,000 tonnes of bird food annually (PFMA, 2018). This is sufficient to feed three times the entire breeding populations of the ten commonest feeder-using bird species year-round if they consumed nothing else (Orros and Fellowes, 2015). There are an average of 100 bird feeders per square kilometre (Cox and Gaston, 2018) equating to one feeder per nine feeder-using birds nationally (Davies et al., 2009). Additionally, there were a minimum of 4.7 million nestboxes in private gardens over a decade ago (Davies et al., 2009), almost one for every pair (1:1.25) of blue (*Cyanistes caeruleus*) and great tit (*Parus major*) - the two most frequent users. While little data is available, several million bird baths are also provisioned (Cox and Gaston, 2018). Provisioning of all forms is increasing and enthusiastically encouraged by UK conservation NGOs like the RSPB, the Wildlife Trusts and the British Trust for Ornithology (Jones, 2011; Jones and Reynolds, 2008), with each apparently receiving financial income from their involvement in the wildlife provisioning market, either by selling own-branded items or officially endorsing partner companies. Garden bird provisioning is marketed as highly beneficial to UK wild birds and proposed as one of the best ways that the public can support wild bird populations (Jones, 2011). Many nature reserves across the UK provision bird food and nestboxes, and nestbox and feeding schemes are standard for both amateur and professional ornithologists' studies, often conducted in areas with lower human population densities, expanding the sphere of provisioning influence (Shutt et al., 2021).

Provisioned foodstuffs have been demonstrated to comprise up to 75% of an individual feeder-using birds' daily diet (Milligan et al., 2017) and provide such an important change in foraging behaviour as to effect morphological evolution (Bosse et al., 2017). Blue tits have been shown to travel several kilometres from their nesting and roosting sites to take advantage of garden bird feeders during spring, a movement-restricted season (Milligan et al., 2017; Shutt et al., 2021). As blue tits are relatively sedentary (Perrins, 1979) in comparison to other more mobile provisioned species, and combined with the UK's high human population density and provisioning rate (Davies et al., 2012), this makes it likely that nearly all individuals of feeder-using species can take advantage of almost unlimited supplementary food (Shutt et al., 2021). Species benefitting from food or nestbox provision can more than triple their breeding density (Mänd et al., 2009; Shutt et al., 2021), with the same species often receiving both forms of provisioning, exacerbating net impacts, and populations of recipient species have increased over the recent past with provisioning (Plummer et al., 2019; Shutt et al., 2021).

Whilst the net effect of provisioning on the populations of most recipient species has been positive, unnatural long-term aggregations has caused novel close-proximity species interactions, facilitating both intra- and inter- specific disease transfer (Lawson et al., 2018; Moyers et al., 2018). A clear example is the crossover of the protozoan parasite *Trichomonas gallinae* from pigeons to finches in 2005, resulting in the rapid spread of the disease trichomoniasis in feeder-using finch populations (Lawson et al., 2018; Robinson et al., 2010). Trichomoniasis precipitated a 66% population reduction in greenfinches *Chloris chloris* over 10 years; a loss of 280,000 individuals annually (Lawson et al., 2018), with chaffinches *Fringilla coelebs* now suffering a similar decline - possibly attributable to *Trichomonas* and *Papillomavirus* infections (Lawson et al., 2018). Passerine salmonellosis incidents are also common in the vicinity of garden feeding (Galbraith et al., 2017b; Lawson et al., 2014). The suspension of supplementary garden bird feeding is reported as the best way to prevent such diseases spreading (Lawson et al., 2018) – perhaps cessation might prevent more arising?

Many species of insectivorous woodland passerines have suffered dramatic declines in the UK in recent years (Fig 2) (Balmer et al., 2013; Massimino et al., 2019). The ranges of these species have often contracted despite habitat availability remaining unchanged, homogenising local avifaunas. The causes of these declines are largely unexplained and often vaguely described as 'varied', 'complex' and 'species-specific'. Among the host of possible causes proffered are: changes in woodland management, reduction in the shrub layer due to over-browsing by a burgeoning deer population, phenological mismatch, and for migratory species, habitat change in African wintering areas or along migratory routes, and contraction from international range edges (Balmer et al., 2013). While each of these likely play a role for different individual species, the empirical evidence is often inconclusive despite frequent tests, and none can be a universal cause across species.

These declines in non-provisioned species have occurred since provisioning has become widespread, and many are either occurring less strongly or not at all in parts of the ranges of the same species where provisioning rates are lower (Keller et al., 2020; Massimino et al., 2019) given reduced human population density (e.g. Sweden) or lower human participation rates (e.g. France). While there is no direct empirical evidence that provisioning has contributed to these declines, its potential role has rarely been raised as a potential driver, yet the ecological pathways by which this could occur are clear (Shutt et al., 2021) and we believe deserving of more research attention (Figs 1, 2). Garden bird feeding is known to change local avifaunas (Fuller et al., 2008; Galbraith et al., 2015; Plummer et al., 2019), is ubiquitous in Britain (Davies et al., 2012; Jones and Reynolds, 2008), and very clear differences in population trajectories have been demonstrated between increasing provisioned species and declining non-provisioned species among woodland insectivores (Shutt et al., 2021). The 40% increase in great tits in the last 25 years (Fig 2), for instance, corresponds to 700,000 additional pairs (to a total of 2.4 million pairs), more than eleven times the entire combined populations of all five declining non-provisioned competitor species depicted in Fig 2, with no concurrent change in background habitat availability. Exclusion experiments clearly demonstrate that the niches of subordinate woodland insectivorous passerines are determined by the presence and abundance of dominant species (Alatalo et al., 1986, 1985), while the breeding density of subordinate species is regulated by the breeding density of dominant competitors through competitive exclusion (Gamelon et al., 2019). Could it be that recent human garden bird provisioning on an enormous scale has tipped the balance of competition within the UK woodland bird community such that a whole raft of rarer, non-provisioned, subordinate species can no longer compete for limited natural resources against abundant, dominant competitor species benefitting from provisioning? Are 700,000 additional pairs of great tits overwhelming the remaining 2,700 pairs of willow tit *Poecile montanus* (Fig 2)?

Marsh (*Poecile palustris*) and willow tits are outcompeted by dominant blue and great tits for both nesting cavities and food resources (Perrins, 1979), and both are, in contrast, less frequent users of supplementary provisions (Shutt et al., 2021). Marsh tits appear able to coexist with the socially dominant species by having a stronger beak that enables them to tackle tougher food resources, by being sedentary and caching (and remembering) food reserves (Perrins, 1979), and by finding novel food sources faster than other tit species (Farine et al., 2015), allowing them to exploit naturally ephemeral resources before being ousted by dominant competitors. All of these competitive advantages are negated by provisioning (Fig 2), which provides their dominant and commoner competitors with unlimited, permanent and static additional resources, enabling them to live at far higher densities (Shutt et al., 2021), increasing competition for natural nesting cavities and food resources.

Similarly, willow tits coexist by their ability to excavate their own nesting holes (Parry and Broughton, 2018; Perrins, 1979). While energetically costly, this enables them to occupy locations where natural holes are scarce, a competitive advantage nullified by nestbox provisioning lifting any limitation imposed by a dearth of natural nesting sites, with inflated provisioned populations of dominant competitors ‘spilling over’ into occupying sub-optimal habitats (Bellamy et al., 2000), such as those previously occupied by willow tits. Eviction from their nesting hole by blue tits is the leading cause of nest failure for willow tits in the UK, responsible for 40% of failures and affecting 23% of nesting attempts, and has likely increased (Parry and Broughton, 2018). Due to the soft nature of the wood excavated, they are also particularly vulnerable to great spotted woodpecker *Dendrocopos major* predation, the second leading cause of nest failure (Parry and Broughton, 2018), also likely increased with inflated great spotted woodpecker populations associated with garden feeding (Massimino et al., 2019) (Fig 2). Lesser spotted woodpeckers *Dryobates minor* similarly suffer from great spotted woodpecker nest predation and nest site eviction (Smith and Smith, 2020) (Fig 2).

Many other declining British insectivorous woodland passerines are likewise subordinate (Shutt et al., 2021), with alternative life history strategies enabling their coexistence, including long-distance migration and open (rather than cavity) nesting, rendered obsolete by provisioning (Fig 2). Despite being energetically demanding and dangerous, migration enables species to avoid competing for very limited natural resources during winter. Provisioning reduces overwinter mortality levels in resident species, removing a key population limitation and improving the physical condition of surviving resident individuals the following spring (Murray et al., 2016; Norris, 1993), nullifying the benefits of migration. Additionally, non-provisioned passerines may also suffer hyperpredation (Courchamp et al., 2000; Roemer et al., 2001) and all significant nest predators, including corvids, squirrels, rats, foxes and great spotted woodpeckers benefit from provisioning, with a concomitant increased risk of nest predation demonstrated in the vicinity of food provisioning (Hanmer et al., 2018, 2017). As provisioning occurs ubiquitously in the UK (Davies et al., 2012), these effects are likely to be widespread, and particularly damaging to species with small populations (Roemer et al., 2001), such as those declining in Fig 2.

While here we use the case study of British garden bird provisioning for illustration, such unbalanced ecosystem dynamics and novel interactions (Fig 1) causing outcompetition would presumably affect all provisioned ecosystems to a varying extent.

5. The time for a change of policy?

There is a lack of unified global policy on human provisioning of wildlife (Baverstock et al., 2019; Jones, 2018), however in a majority of countries, including the UK and USA, it is encouraged by conservation organisations, frequently justified as being beneficial to biodiversity conservation (Jones, 2011). Short-term targeted provisioning of threatened species is a proven conservation intervention (Bolam et al., 2020; Olaciregui et al., 2020), however, we are unaware of instances where generalised provisioning has averted extinctions. Additionally, long-term artificial provision dependency in threatened populations is undesirable and suggests a failure of conservation action to provide sufficient natural resources to support natural populations.

The possibilities for generalised provisioning to erode biodiversity, by altering competitive interactions (Figs 1, 2), contributing to biotic homogenisation in human-modified landscapes (Newbold et al., 2019), have been largely ignored and we believe merits urgent empirical research. Foraging niche overlap has traditionally been difficult to quantify, but the advent of faecal metabarcoding could enable clearer insights if competitor diets are assessed simultaneously (Shutt et al., 2020). Comparison of the influence of competition (e.g. nest eviction and exclusion, productivity and survival rates) could also be conducted between areas with high incidences of provisioning versus those with low, possibly through international project collaboration.

Species within ecological communities coexisted before widespread interventional provisioning and therefore human wardening of wildlife, while well-intentioned, ingrained and espoused by many conservation organisations, may be unmerited and delivering unintended negative consequences. We posit that the positive human aspects of provisioning and encouragement of engagement with nature could equally be achieved by more natural alternatives to provisioning, including wildlife gardening and natural habitat provision (Luck et al., 2011), or by limited provisioning.

Weighing the advantages and disadvantages of supplementary wildlife provisioning (Table 2), we would recommend a more cautious approach to the encouragement of the activity, particularly generalised provisioning (Baverstock et al., 2019). While generalised provisioning may boost alpha diversity in urban environs (Plummer et al., 2019), due to the movements of recipients the impact is unlikely to be contained and might reduce beta and gamma diversity (Shutt et al., 2021) (Fig S1). Importantly, we believe that the effects of provisioning should not solely be considered an urban phenomenon and effects on provisioned species should no longer be assessed irrespective of the inevitable consequential effects upon their competitors, prey and predators.

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Table 1. Partitioning forms of provisioning along two lines of differentiation to form a unified theoretical framework: targeted or generalised provisioning, providing replacement or additional resources, with definitions, examples and frequent motivations of each.

	Targeted provisioning	Generalised provisioning
Replacement resources	Providing resources to specific species which have been lost to them in the natural environment, often following disturbance. Examples: • Nestbox provision to glossy-black cockatoos after logging and fires • Nestbox provisioning to Santa Marta parakeets following removal of their nesting trees • Water provision to koalas following drought Motivations: conservation intervention to maintain or boost populations of threatened species References: Garnett et al., 1999; González et al., 2006; Olaciregui et al., 2020	Providing resources necessary for multiple species which have been lost in the landscape, aimed at wildlife in general. Examples: • Winter seed crop provision to farmland birds following agricultural intensification • Vulture restaurants following removal of natural carrion • Garden pond creation following the destruction of natural ponds Motivations: conservation intervention to support ecological communities after a general loss of resources. References: Bolam et al., 2020; Brock et al., 2017; Cortés-Avizanda et al., 2016
Additional resources	Providing resources to specific species which are additional to those naturally available, often to boost populations or attract individuals. Examples: • Food provision to kakapo to boost the productivity of this endangered species • Food provision to great white sharks and antpittas to attract them to areas for paying tourists to view • Baiting ungulate species for hunting purposes Motivations: attracting species to designated areas for viewing by tourists, study by researchers, or baiting for hunting. Also to boost populations of threatened species. References: Burgin and Hardiman, 2015; Clout et al., 2002; Selva et al., 2014; Woods et al., 2010	Providing resources for multiple species and communities which are additional to those naturally available. Examples: • Waterhole provision in dry landscapes to attract and boost numbers of large mammals, often for tourism or hunting • Nesting chamber provision to bees to boost pollinator populations • Food and excess nestbox provision to garden birds and mammals to facilitate human-wildlife interaction and enjoyment Motivations: nurturing feelings of people trying to help ‘their’ wildlife, both for the sake of the wildlife and the pleasure value of wildlife interaction, and to boost and concentrate animal numbers for tourism and hunting purposes. References: Brock et al., 2017; Cox and Gaston, 2018; Tshipa et al., 2017

Table 2. Benefits and costs associated with provisioning wildlife for the provisioner and the recipient, alongside proposed indirect ecosystem impacts.

	Benefits	Costs
Effects on provisioner	• Enjoyment value of wildlife interaction • Improved mental health, wellbeing and relaxation • Link to, and engagement with, nature References: Brock et al., 2017; Cox and Gaston, 2018; Luck et al., 2011	• Monetary and time costs of provisioning • Human-wildlife conflict if undesirable species are encouraged • Zoonotic disease transfer References: Cox et al., 2018; Cox and Gaston, 2018; Lawson et al., 2014
Effects on provisioned recipient	• Increased survival rates, particularly overwinter • Increased productivity and reproductive success • Increased individual health and quality and reduced parasites • Increased breeding densities • Increased populations and abundance • Increased ranges and residency/reduced need to migrate References: Fuller et al., 2008; Greig et al., 2017; Plummer et al., 2019; Robb et al., 2008a; Shutt et al., 2021a; Wilcoxen et al., 2015	• Increased intraspecific disease transmission risk • Increased predation risk by both natural predators and domestic pets • Increased window and road collisions • Possible dependency, poor nutrition, sperm defects and blood chemistry changes References: Ishigame et al., 2006; Kummer and Bayne, 2015; Lawson et al., 2018; Pavisse et al., 2019; Støstad et al., 2019; Swallow et al., 2019
Indirect ecosystem effects	• Increased prey for predators of recipient taxa • Enhanced environmental awareness and pro-environment behaviours of provisioners	• Increased competition over natural resources, reduced competitor populations • Ecosystem homogenisation by favouring certain species at the expense of others • Increased interspecific disease transfer • Hyperpredation on natural prey of recipient taxa • Hyperpredation on non-provisioned competitor species • Mesopredator release following unintentional provisioning • Increased community takeover by dominant and/or non-native invasive taxa • Ecological footprint of growing and transporting provisions

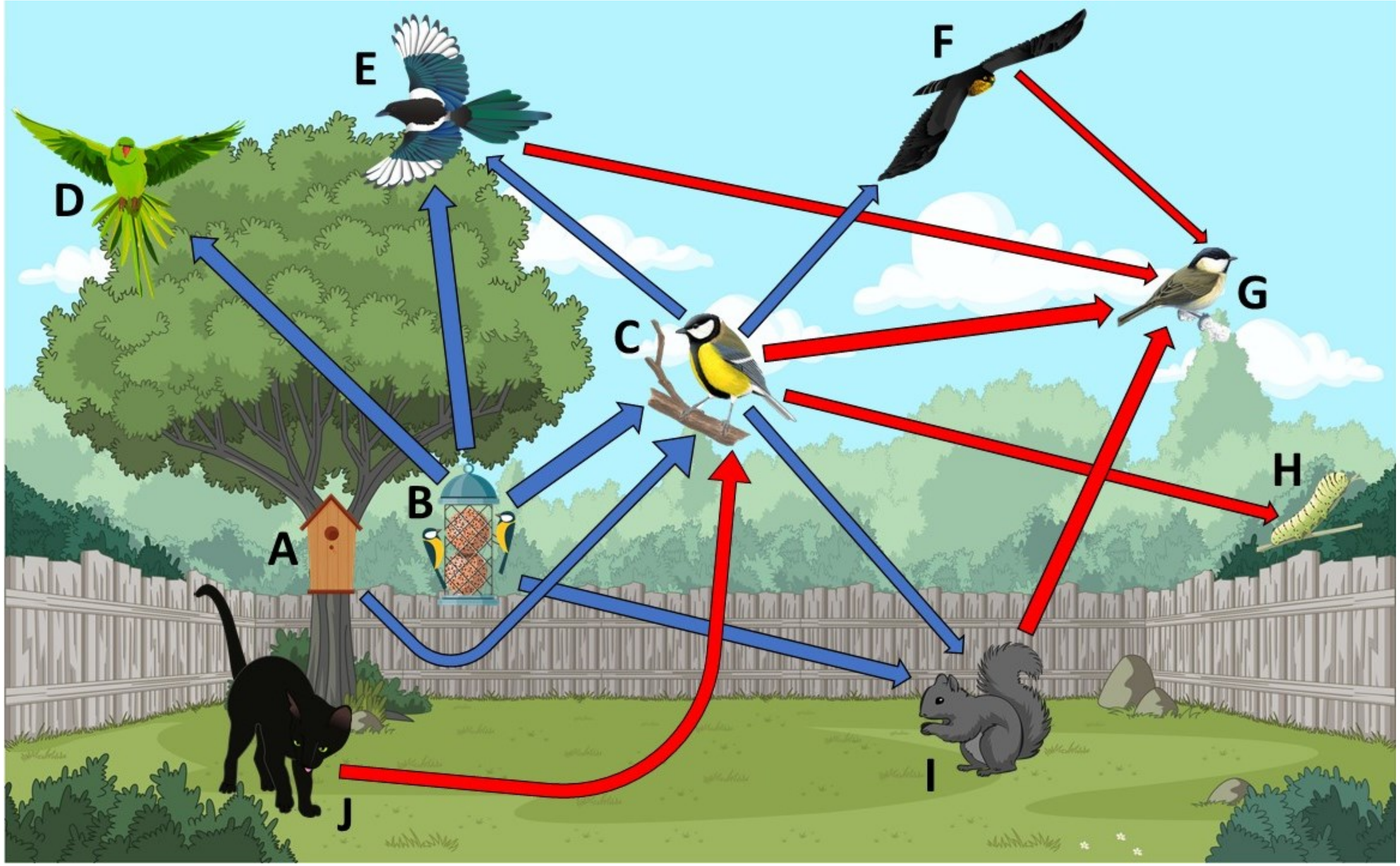
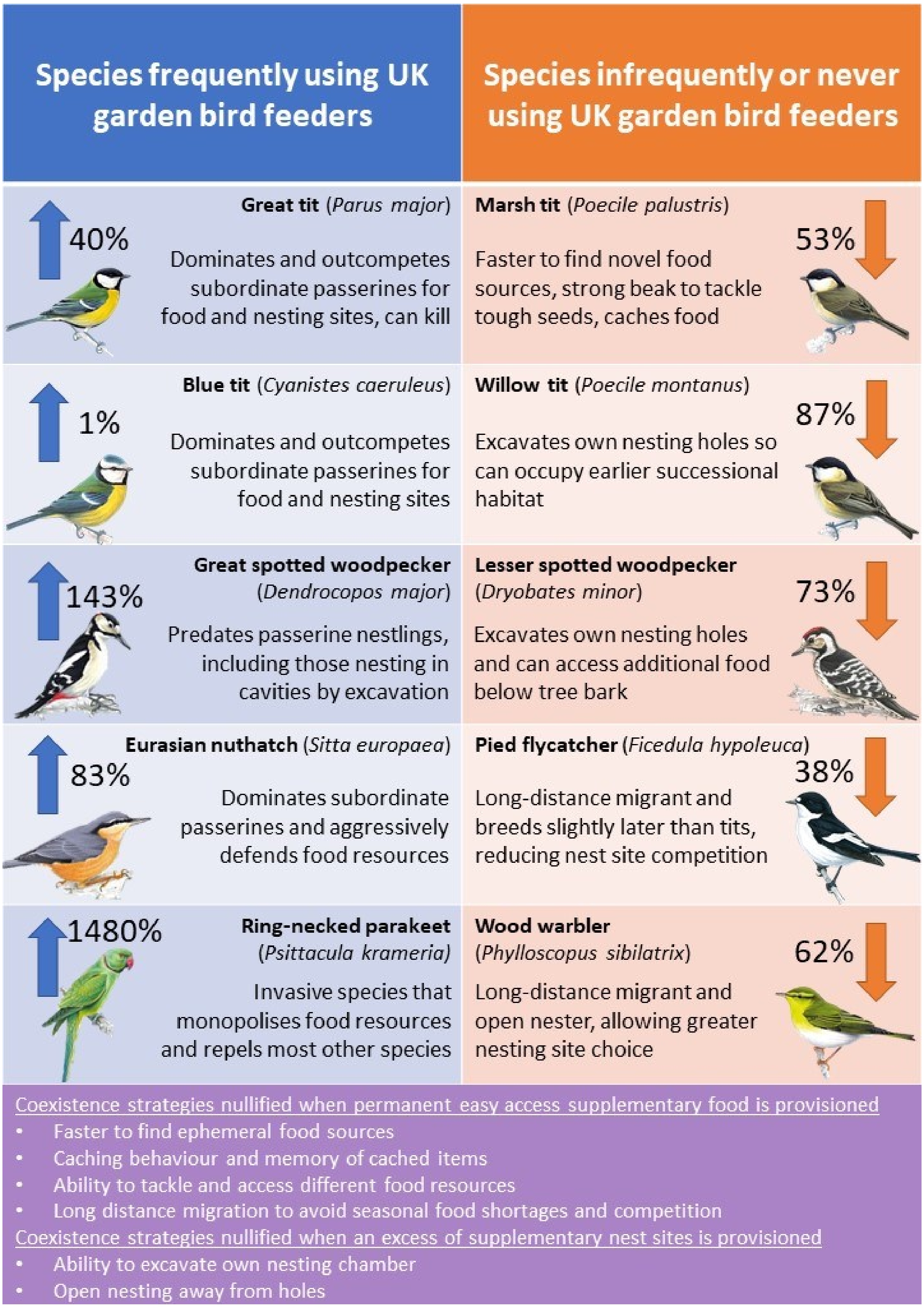


Fig 1 Schematic illustrating novel interactions facilitated by garden bird provisioning. All arrows indicate predation with the exception of the one between C and G which indicates competition. Red arrows indicate a negative effect while blue arrows indicate a positive effect. Arrow size is not indicative of effect size and illustrations are not to scale. A) provisioned nestbox B) provisioned food C) intended provision recipient D) non-native invasive recipient E) natural omnivorous mesopredator F) natural carnivorous predator G) non-provisioned competitor of recipient H) natural prey I) non-native invasive omnivorous mesopredator J) domestic pet predator. Individual illustrations purchased from istockphoto.com and adapted.



Species frequently using UK garden bird feeders	Species infrequently or never using UK garden bird feeders
↑ 40% **Great tit** (*Parus major*) Dominates and outcompetes subordinate passerines for food and nesting sites, can kill	**Marsh tit** (*Poecile palustris*) 53% ↓ Faster to find novel food sources, strong beak to tackle tough seeds, caches food
↑ 1% **Blue tit** (*Cyanistes caeruleus*) Dominates and outcompetes subordinate passerines for food and nesting sites	**Willow tit** (*Poecile montanus*) 87% ↓ Excavates own nesting holes so can occupy earlier successional habitat
↑ 143% **Great spotted woodpecker** (*Dendrocopos major*) Predates passerine nestlings, including those nesting in cavities by excavation	**Lesser spotted woodpecker** (*Dryobates minor*) 73% ↓ Excavates own nesting holes and can access additional food below tree bark
↑ 83% **Eurasian nuthatch** (*Sitta europaea*) Dominates subordinate passerines and aggressively defends food resources	**Pied flycatcher** (*Ficedula hypoleuca*) 38% ↓ Long-distance migrant and breeds slightly later than tits, reducing nest site competition
↑ 1480% **Ring-necked parakeet** (*Psittacula krameria*) Invasive species that monopolises food resources and repels most other species	**Wood warbler** (*Phylloscopus sibilatrix*) 62% ↓ Long-distance migrant and open nester, allowing greater nesting site choice

Coexistence strategies nullified when permanent easy access supplementary food is provisioned

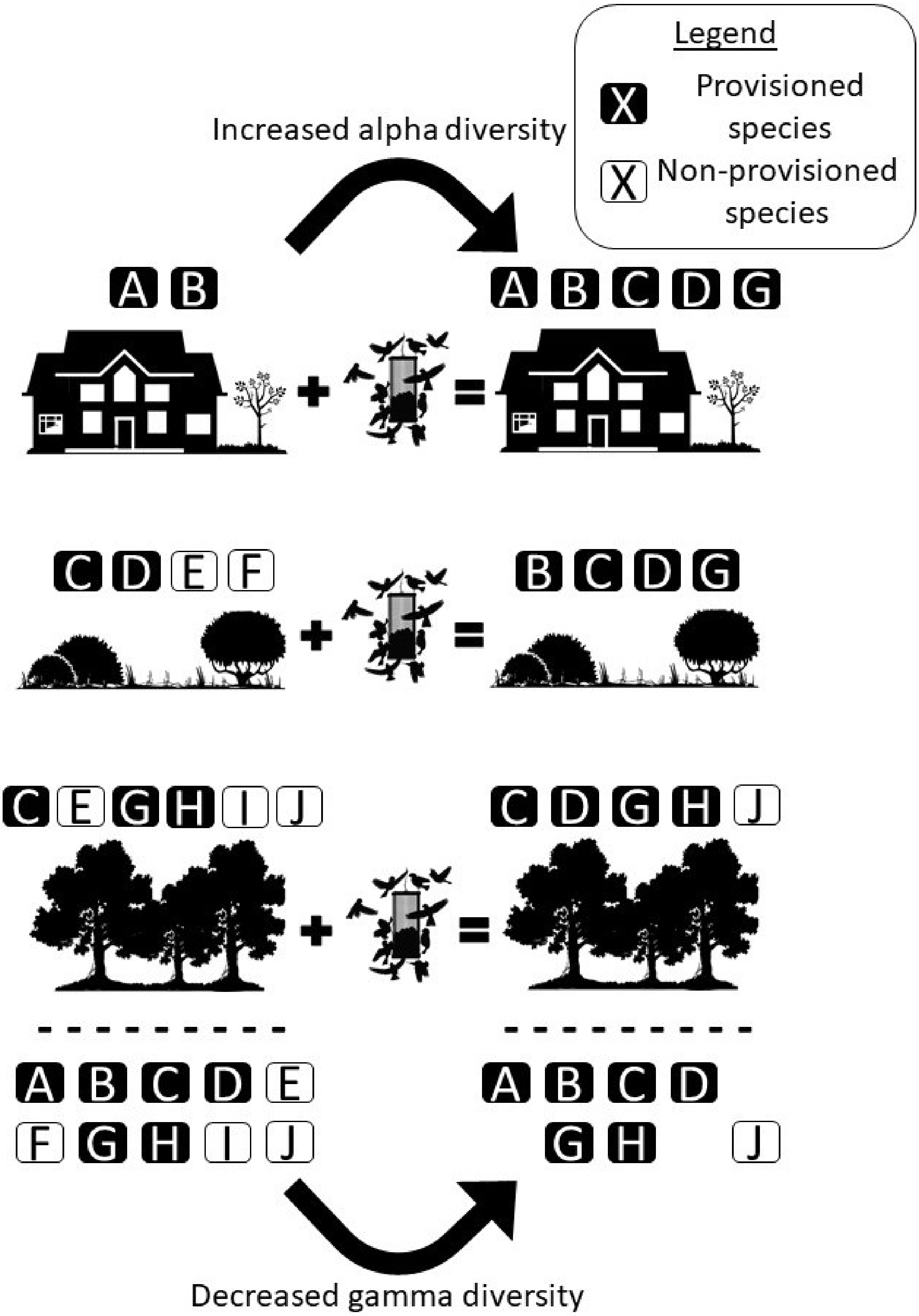
- Faster to find ephemeral food sources
- Caching behaviour and memory of cached items
- Ability to tackle and access different food resources
- Long distance migration to avoid seasonal food shortages and competition

Coexistence strategies nullified when an excess of supplementary nest sites is provisioned

- Ability to excavate own nesting chamber
- Open nesting away from holes

Fig 2 Representative UK woodland bird species that regularly take advantage of garden bird food provisioning (left, blue) and those that don't or only do so infrequently (right, orange). Population trends (25-year) are depicted (Massimino et al., 2019) along with traits that either facilitate outcompeting other species (left) or traits that enable coexistence (right), with explanations of how coexistence traits are negated by human provisioning (bottom, purple). Illustrations by Mike Langman and purchased for use from RSPB images.

Supplementary online material



Supplementary Fig 1 Hypothetically demonstrating how the addition of nearby bird feeders to three different habitats can simultaneously increase local alpha diversity at urban sites while decreasing overall gamma diversity. This occurs by reducing beta diversity and homogenising the communities occupying all the habitats due to asymmetrically favouring species that take advantage of bird feeders. In the example, supplementary feeding at the urban location has added species C, D and G, which take advantage of the feeders, to the local species pool, increasing local alpha diversity. However, while supplementary feeding at the woodland site has enabled species D to colonise, species E and I, which don’t use the feeders, have been eliminated from the local species pool due to outcompetition from species that do use the supplementary feeders. Feeders in this example have therefore led to the communities of the urban and woodland locations becoming more similar (lower beta diversity). This has lowered the total diversity across the three locations combined as soon species have been eliminated (lower gamma diversity). Individual illustrations purchased from istockphoto.com and adapted.