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

3
4 **Keywords:** Bird feeding, competition, hyperpredation, supplementary resources, human-wildlife
5 interaction, biotic homogenisation

6
7 **Abstract**

8
9 Provisioning of wildlife with food, water and breeding sites is a globally ubiquitous phenomenon.
10 While some provisioning is targeted at single species of conservation concern, generalised
11 provisioning is more common and can exceed the local availability of natural resources for recipient
12 taxa. Generalised provisioning is enthusiastically promoted by many conservation organisations as a
13 means to foster connection with nature and help wildlife. However, such a vast input of additional
14 resources into the environment must have diverse, ecosystem-wide consequences. Direct effects
15 upon recipient taxa have garnered most research interest, and are generally positive in leading to
16 increased survival, productivity and hence population growth. However, we argue that the wider
17 implications for the recipients' non-provisioned competitors, prey and predators are
18 underappreciated and have the potential to generate pervasive negative impacts for biodiversity.
19 The impact of provisioning has also hitherto been considered predominantly in urban contexts,
20 overlooking the movements of wildlife to and from provisioning sources and the widespread nature
21 of both human settlements and provisioning, underappreciating the potential scale of impact. Using
22 a case study of UK garden bird food and nestbox provisioning, we hypothesise how well-intentioned
23 provisioning could be contributing to widespread ecological community change and
24 homogenisation. This may consequently help drive declines in species of conservation concern by
25 asymmetrically benefitting common and adaptable species, leaving their competitors exposed to
26 enhanced direct competition, hyperpredation, mesopredator release and heightened disease
27 transmission risks. We recommend further research into these ecosystem cascades and a more
28 cautious, evidence-based approach to the encouragement of provisioning wildlife.

29
30 **1. Introduction**

31
32 Intentional human provisioning of wildlife with food, water, shelter and nesting sites occurs
33 worldwide and constitutes a growing, multi-billion-dollar industry especially prevalent in western
34 culture (Cox and Gaston, 2018; Jones and Reynolds, 2008). Provisioning takes many forms and
35 targets almost every major taxonomic group, from bee hotels (MacIvor and Packer, 2015) through
36 vulture restaurants (Cortés-Avizanda et al., 2016) and shark baiting for tourists (Burgin and
37 Hardiman, 2015; Maljković and Côté, 2011), to waterhole creation for large mammals in arid regions
38 (Landman et al., 2012; Tshipa et al., 2017). While types of provisioning are numerous and diverse
39 and have generally been treated disparately, they all share unifying features and are components of
40 the same socioecological phenomenon.

41
42 We believe that the varying types of provisioning can be grouped into four discrete categories along
43 two axes of divergence: (i) targeted provisioning to benefit a specific taxon, or generalised
44 provisioning, and (ii) providing replacement resources, or additional resources (Table 1). The
45 motivations for wildlife provisioning are diverse and differ by provisioning category (Table 1), but are
46 primarily well-intentioned (Brock et al., 2017; Cox and Gaston, 2018). Although there is some
47 disagreement (Baverstock et al., 2019; Jones, 2018), provisioning is often regarded by both the
48 public and conservationists as beneficial for biodiversity conservation (Davies et al., 2012; Jones,
49 2011; Jones and Reynolds, 2008).

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

65
66 The massive scale of this resource input likely has significant ecosystem impacts (Jones, 2018; Jones
67 and Reynolds, 2008), and while direct effects on provisioned taxa have garnered some research
68 interest, we contend that the indirect implications are poorly understood. Despite this knowledge
69 gap, wildlife provisioning is actively encouraged by many conservation organisations in many, but
70 not all, countries (Baverstock et al., 2019; Hanmer et al., 2017; Jones, 2011), including the National
71 Wildlife Federation in the USA and the Royal Society for the Protection of Birds (RSPB) in the UK.
72 Herein, we review documented impacts of wildlife provisioning alongside proposing hitherto
73 overlooked and understudied ecosystem cascades to ascertain whether these activities help or
74 hinder biodiversity conservation efforts. We focus on examples involving generalised provisioning of
75 additional resources (Table 1) as this is the commonest, most impactful and least regulated form,
76 but across provisioning forms we would expect similar ecological interactions to be occurring on
77 varying scales.

78

79 **2. Known direct impacts of wildlife provisioning**

80

81 **2.1. Positive direct impacts**

82

83 Research into the direct benefits and costs of provisioning upon recipient individuals and species
84 constitutes the majority of work into wildlife provisioning to date. The fitness of food-provisioned
85 individuals often increases, with increased productivity and offspring survival rates (González et al.,
86 2006; Robb et al., 2008b), reduced likelihood of starvation and health complications (Chamberlain et
87 al., 2009; Knutie, 2020; Wilcoxon et al., 2015), enhanced immune function (Strandin et al., 2018) and
88 increased survivorship (Murray et al., 2016; Norris, 1993). Provisioned nestboxes lift limitations from
89 the restricted availability of natural breeding sites (MacIvor and Packer, 2015; Mänd et al., 2009),
90 increase population densities and can raise breeding success (East and Perrins, 1987). Populations of
91 many species provisioned with food or nestboxes have therefore increased at local and regional
92 scales (Mänd et al., 2009; Plummer et al., 2019) (Table 2). Food and water provisioning is particularly
93 beneficial in nutritionally limited, drought susceptible or energetically costly environments (Robb et
94 al., 2008a; Tshipa et al., 2017). This can even lead to loss or alteration of migratory behaviour by
95 allowing individuals to persist in regions year-round that were previously seasonally uninhabitable
96 (Greig et al., 2017; Páez et al., 2018; Plummer et al., 2015; Satterfield et al., 2018).

97

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

102 Replacement feeding for vultures which have lost natural resources due to human activity, and to
103 steer them away from contaminated food, is also allowing threatened populations to persist (Cortés-
104 Avizanda et al., 2016). Additional feeding of several threatened species under population
105 management programs has allowed them to expand and/or recolonise former ranges, conferring
106 greater resistance to stochastic events (Clout et al., 2002; González et al., 2006), as has nestbox
107 provision (Carstens et al., 2019). Reintroductions of species of conservation concern often rely on
108 initial additional resource provisioning to encourage population persistence (Cortés-Avizanda et al.,
109 2016; Piper et al., 1999). Indeed, targeted provisioning actions have been among a portfolio of
110 interventions that have saved species including pink pigeon *Nesoenas mayeri*, California condor
111 *Gymnogyps californianus* and orange-bellied parrot *Neophema chrysogaster* from extinction (Bolam
112 et al., 2020). We are however unaware of any species saved from extinction through generalised
113 provisioning.

114
115 Provisioning wildlife has also been shown to have important and positive consequences for the
116 provisioner (Table 2). It has been described as a vital link to nature in an increasingly urbanised and
117 nature-disconnected world (Brock et al., 2017; Jones, 2018). Provisioners show greater
118 environmental awareness than non-provisioners and report increased feelings of connection to
119 nature (Cox and Gaston, 2016; Davies et al., 2012) which may foster pro-environmental behaviours
120 in other aspects of life (Cox and Gaston, 2016). Provisioners report being more relaxed due to their
121 engagement with nature and benefit from improved wellbeing and mental health (Cox and Gaston,
122 2016), while citizen science bird feeding schemes also gather useful scientific data (Jones and
123 Reynolds, 2008).

124 125 **2.2. Negative direct impacts**

126
127 In addition to the direct positive impacts of resource provisioning upon recipients, some direct
128 negative consequences are also documented (Table 2). Increased intraspecific disease transmission
129 is associated with large and persistent aggregations around provisioned food sources (Hochachka
130 and Dhondt, 2000; Lawson et al., 2018; Moyers et al., 2018). Generalised provisioning encourages
131 novel interspecific associations which facilitates novel interspecific disease crossovers, which have
132 already driven large declines in some species (Lawson et al., 2018, 2014; Robinson et al., 2010).
133 Diseases can also spread from provisioned wildlife to provisioning humans (Lawson et al., 2014).
134 Elevated wildlife mortality rates around provisioned food may occur (Pavisse et al., 2019; Swallow et
135 al., 2019), with predation by domestic pets as well as window collisions exacerbated by encouraging
136 wildlife into the vicinity of human settlements (Kummer and Bayne, 2015; Pavisse et al., 2019). The
137 reproductive success of recipients might also be negatively affected if they become dependent upon
138 provisioned food resources of poor nutritive value (Chamberlain et al., 2009; Plummer et al., 2013),
139 which can affect blood chemistry (Ishigame et al., 2006; Støstad et al., 2019) with unknown health
140 impacts. Nestboxes can be associated with an increased bacterial load and egg mortality compared
141 to natural cavities (Devaynes et al., 2018), owing to different internal microclimates.

142
143 Provisioned resources of all types are often monopolised by dominant individuals and species,
144 resulting in the exclusion of others from local assemblages (East and Perrins, 1987; Francis et al.,
145 2018; Maljković and Côté, 2011; Parsons et al., 2006) (Table 2). Monopolising species are typically
146 abundant generalists well adapted to anthropogenic environments, and often include alien species
147 for which provisioning can aid invasion (Galbraith et al., 2017a, 2015; Le Louarn et al., 2016; MacIvor
148 and Packer, 2015). As invasive species are one of the most significant causes of extinctions globally
149 (Bolam et al., 2020) this may be of significant concern. Habitat damage can also occur when resource
150 provisioning enables persistent gatherings or ecologically unsustainable populations of recipient
151 species to persist (Cooper et al., 2006; Landman et al., 2012). Pollination services can even be
152 reduced due to distraction by provisioned foodstuffs, which may impact vegetation (du Plessis et al.,

153 2021; Páez et al., 2018). A subtle negative impact is that food provisioning can lead to biased
154 offspring sex ratios, a particular problem for Critically Endangered populations (Clout et al., 2002).

155
156 **3. Our contention – indirect impacts may be far more pervasive than currently appreciated**

157
158 Research into the effects of wildlife provisioning has tended to focus on provisioned species,
159 neglecting sympatric non-provisioned species. We contend that this bias overlooks trophic cascades,
160 as providing one organism with additional resources impacts all other organisms connected to it in
161 the food web; be they predators, prey, pathogens, parasites or competitors, if these exist in the
162 ecosystem. These interactions may then promote negative ecosystem impacts on biodiversity that
163 have hitherto received scant attention (Table 2).

164
165 Increasing populations of provisioned species will provide greater prey abundance for their natural
166 predators and may facilitate an increase in predator populations (Courchamp et al., 2000; Pintor and
167 Byers, 2015; Roemer et al., 2001). As most predators are generalists, increased predator populations
168 supported by artificially inflated populations of provisioned prey species may result in
169 hyperpredation on non-provisioned prey species (Courchamp et al., 2000; Lees and Bell, 2008;
170 Maeda et al., 2019). This could cause declines in the latter, particularly if the non-provisioned prey
171 species exist at low densities (Lurgi et al., 2018; Roemer et al., 2001) (Fig 1, Table 2). Equally,
172 predation by inflated populations of provisioned species may directly hyperpredate their own
173 natural prey resources (Orros et al., 2015; Orros and Fellowes, 2012) (Fig 1).

174
175 Hyperpredation of non-provisioned species may be further exacerbated by mesopredator release,
176 following the (often unintended) provisioning of members of this guild, such as corvids, gulls, foxes
177 and rodents (Chamberlain et al., 2009; Hanmer et al., 2017; Reed and Bonter, 2018). While
178 mesopredator release is usually considered in the context of the removal of regulatory apex
179 predators, the opportunistic use of provisioning by this guild may additionally boost their
180 populations (Coates et al., 2020; Hanmer et al., 2017). Mesopredators are common predators of bird
181 eggs and chicks and young mammals and their population increases due to human activities have
182 been linked to declines in many species globally (Coates et al., 2020; Hanmer et al., 2017), reducing
183 biodiversity (Oro et al., 2013) (Fig 1).

184
185 A potentially pervasive threat to biodiversity caused by provisioning is increased competition for
186 natural resources between inflated populations of provisioned species and their non-provisioned
187 competitor species (Jones, 2018; Shutt et al., 2021) (Fig 1). Co-occurring species within assemblages
188 compete with each other for limited natural resources but coexist by exploiting subtly different
189 niches and employing varying life-history strategies, each with associated costs and benefits.
190 Provisioning may reduce or eliminate advantages from alternative life history strategies occupied by
191 non-provisioned species, reducing the ability of these species to compete and coexist, for example
192 by reducing the benefits of migration by providing permanent and static artificial resources (Greig et
193 al., 2017; Plummer et al., 2015). Provisioned species could then outcompete competitors for natural
194 resources due to the advantages gained from provisioning (Francis et al., 2018; Galbraith et al.,
195 2015), reducing the number of ecological niches available and hence impoverishing community
196 biodiversity (for specific examples to illustrate these abstract points please refer to section 4). This
197 may be particularly impactful in small forest fragments where threatened species are increasingly
198 being provisioned to allow tourists to view them (Woods et al., 2010), but where competition
199 impacts are probably very important in structuring communities.

200
201 Community takeover by dominant species due to human food provisioning is well documented in
202 Australia where boisterous despotic competitor species such as noisy miner *Manorina*
203 *melanocephala* monopolise supplemental resources, enabling them to actively and aggressively

204 exclude other species (Jones, 2018; Parsons et al., 2006). Equally, in New Zealand, supplementary
205 bird food provisioning disproportionately benefits alien invasive species which consequently further
206 outcompete and replace native species (Galbraith et al., 2017a, 2015). Conservation organisations in
207 both countries are subsequently anti-provisioning, in contrast to general international attitudes
208 (Baverstock et al., 2019). Such impacts of competition may be less overt in other regions, but they
209 will inevitably exist if some species are provided with additional (and often comparatively unlimited)
210 resources not available to their natural competitors (Francis et al., 2018).

211
212 Community assemblage changes due to provisioning have been demonstrated (Fuller et al., 2008;
213 Galbraith et al., 2015; Plummer et al., 2019), although these exclusively consider urban ecosystems.
214 These studies have demonstrated supplementary feeding attracting novel species and restructuring
215 the community towards a predominance of feeder-using species (Fig S1), or nestbox-using species
216 (MacIvor and Packer, 2015). While important, this urban focus ignores the large movements and
217 migrations of animals to and from provisioning sources (Greig et al., 2017; Milligan et al., 2017), the
218 widespread nature of human settlements and provisioning (Hanmer et al., 2017), higher provisioning
219 rates often occurring in rural communities (Davies et al., 2012), and that nature reserve
220 management frequently includes provisioning to enhance visitor experience (Woods et al., 2010).
221 Effects are therefore likely to occur across a far wider spatial extent than currently appreciated
222 (Shutt et al., 2021), favouring novel provision-using community assemblages across large areas
223 (Galbraith et al., 2015). As provisioned species are often abundant, adaptable and widespread,
224 similar species benefit ubiquitously across wide geographic areas, and different types of provisioning
225 may benefit the same species' and exacerbate net impacts, this may contribute to the
226 homogenisation of ecological communities (Newbold et al., 2019; Oro et al., 2013), reducing beta
227 and gamma diversity, even if local alpha diversity increases (Fig S1).

228
229 Lastly, the ecological footprint of provisioning must be considered as an indirect impact. Carbon and
230 land use costs in creating and transporting provisioned food are large (Lin, 2005). Land supporting
231 agriculture and forestry used for provisioning replaces land that could be used for human agriculture
232 and forestry, which may drive further habitat loss. As some provisions are produced in tropical
233 countries (e.g. Niger seed (Lin, 2005)) the biodiversity costs of crop growth in more biodiverse
234 regions could outweigh any benefits bestowed upon recipient species in less biodiverse areas where
235 provisioning is conducted.

236
237 Combined, and with the massive scale of provisioning, we consider that these indirect impacts could
238 potentially be playing a significant role in ecological community changes, contributing to biotic
239 homogenisation and even local extinctions (Newbold et al., 2019; Oro et al., 2013).

240

241 **4. Case study: UK garden bird provisioning**

242

243 Over 17 million UK households (64%) (Davies et al., 2012) spend a combined £250 million on more
244 than 150,000 tonnes of bird food annually (PFMA, 2018). This is sufficient to feed three times the
245 entire breeding populations of the ten commonest feeder-using bird species year-round if they
246 consumed nothing else (Orros and Fellowes, 2015). There are an average of 100 bird feeders per
247 square kilometre (Cox and Gaston, 2018) equating to one feeder per nine feeder-using birds
248 nationally (Davies et al., 2009). Additionally, there were a minimum of 4.7 million nestboxes in
249 private gardens over a decade ago (Davies et al., 2009), almost one for every pair (1:1.25) of blue
250 (*Cyanistes caeruleus*) and great tit (*Parus major*) - the two most frequent users. While little data is
251 available, several million bird baths are also provisioned (Cox and Gaston, 2018). Provisioning of all
252 forms is increasing and enthusiastically encouraged by UK conservation NGOs like the RSPB, the
253 Wildlife Trusts and the British Trust for Ornithology (Jones, 2011; Jones and Reynolds, 2008), with
254 each apparently receiving financial income from their involvement in the wildlife provisioning

255 market, either by selling own-branded items or officially endorsing partner companies. Garden bird
256 provisioning is marketed as highly beneficial to UK wild birds and proposed as one of the best ways
257 that the public can support wild bird populations (Jones, 2011). Many nature reserves across the UK
258 provision bird food and nestboxes, and nestbox and feeding schemes are standard for both amateur
259 and professional ornithologists' studies, often conducted in areas with lower human population
260 densities, expanding the sphere of provisioning influence (Shutt et al., 2021).

261
262 Provisioned foodstuffs have been demonstrated to comprise up to 75% of an individual feeder-using
263 birds' daily diet (Milligan et al., 2017) and provide such an important change in foraging behaviour as
264 to effect morphological evolution (Bosse et al., 2017). Blue tits have been shown to travel several
265 kilometres from their nesting and roosting sites to take advantage of garden bird feeders during
266 spring, a movement-restricted season (Milligan et al., 2017; Shutt et al., 2021). As blue tits are
267 relatively sedentary (Perrins, 1979) in comparison to other more mobile provisioned species, and
268 combined with the UK's high human population density and provisioning rate (Davies et al., 2012),
269 this makes it likely that nearly all individuals of feeder-using species can take advantage of almost
270 unlimited supplementary food (Shutt et al., 2021). Species benefitting from food or nestbox
271 provision can more than triple their breeding density (Mänd et al., 2009; Shutt et al., 2021), with the
272 same species often receiving both forms of provisioning, exacerbating net impacts, and populations
273 of recipient species have increased over the recent past with provisioning (Plummer et al., 2019;
274 Shutt et al., 2021).

275
276 Whilst the net effect of provisioning on the populations of most recipient species has been positive,
277 unnatural long-term aggregations has caused novel close-proximity species interactions, facilitating
278 both intra- and inter- specific disease transfer (Lawson et al., 2018; Moyers et al., 2018). A clear
279 example is the crossover of the protozoan parasite *Trichomonas gallinae* from pigeons to finches in
280 2005, resulting in the rapid spread of the disease trichomoniasis in feeder-using finch populations
281 (Lawson et al., 2018; Robinson et al., 2010). Trichomoniasis precipitated a 66% population reduction
282 in greenfinches *Chloris chloris* over 10 years; a loss of 280,000 individuals annually (Lawson et al.,
283 2018), with chaffinches *Fringilla coelebs* now suffering a similar decline - possibly attributable to
284 *Trichomonas* and *Papillomavirus* infections (Lawson et al., 2018). Passerine salmonellosis incidents
285 are also common in the vicinity of garden feeding (Galbraith et al., 2017b; Lawson et al., 2014). The
286 suspension of supplementary garden bird feeding is reported as the best way to prevent such
287 diseases spreading (Lawson et al., 2018) – perhaps cessation might prevent more arising?

288
289 Many species of insectivorous woodland passerines have suffered dramatic declines in the UK in
290 recent years (Fig 2) (Balmer et al., 2013; Massimino et al., 2019). The ranges of these species have
291 often contracted despite habitat availability remaining unchanged, homogenising local avifaunas.
292 The causes of these declines are largely unexplained and often vaguely described as 'varied',
293 'complex' and 'species-specific'. Among the host of possible causes proffered are: changes in
294 woodland management, reduction in the shrub layer due to over-browsing by a burgeoning deer
295 population, phenological mismatch, and for migratory species, habitat change in African wintering
296 areas or along migratory routes, and contraction from international range edges (Balmer et al.,
297 2013). While each of these likely play a role for different individual species, the empirical evidence is
298 often inconclusive despite frequent tests, and none can be a universal cause across species.

299
300 These declines in non-provisioned species have occurred since provisioning has become widespread,
301 and many are either occurring less strongly or not at all in parts of the ranges of the same species
302 where provisioning rates are lower (Keller et al., 2020; Massimino et al., 2019) given reduced human
303 population density (e.g. Sweden) or lower human participation rates (e.g. France). While there is no
304 direct empirical evidence that provisioning has contributed to these declines, its potential role has
305 rarely been raised as a potential driver, yet the ecological pathways by which this could occur are

306 clear (Shutt et al., 2021) and we believe deserving of more research attention (Figs 1, 2). Garden bird
307 feeding is known to change local avifaunas (Fuller et al., 2008; Galbraith et al., 2015; Plummer et al.,
308 2019), is ubiquitous in Britain (Davies et al., 2012; Jones and Reynolds, 2008), and very clear
309 differences in population trajectories have been demonstrated between increasing provisioned
310 species and declining non-provisioned species among woodland insectivores (Shutt et al., 2021). The
311 40% increase in great tits in the last 25 years (Fig 2), for instance, corresponds to 700,000 additional
312 pairs (to a total of 2.4 million pairs), more than eleven times the entire combined populations of all
313 five declining non-provisioned competitor species depicted in Fig 2, with no concurrent change in
314 background habitat availability. Exclusion experiments clearly demonstrate that the niches of
315 subordinate woodland insectivorous passerines are determined by the presence and abundance of
316 dominant species (Alatalo et al., 1986, 1985), while the breeding density of subordinate species is
317 regulated by the breeding density of dominant competitors through competitive exclusion (Gamelon
318 et al., 2019). Could it be that recent human garden bird provisioning on an enormous scale has
319 tipped the balance of competition within the UK woodland bird community such that a whole raft of
320 rarer, non-provisioned, subordinate species can no longer compete for limited natural resources
321 against abundant, dominant competitor species benefitting from provisioning? Are 700,000
322 additional pairs of great tits overwhelming the remaining 2,700 pairs of willow tit *Poecile montanus*
323 (Fig 2)?

324

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

336

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

350

351 Many other declining British insectivorous woodland passerines are likewise subordinate (Shutt et
352 al., 2021), with alternative life history strategies enabling their coexistence, including long-distance
353 migration and open (rather than cavity) nesting, rendered obsolete by provisioning (Fig 2). Despite
354 being energetically demanding and dangerous, migration enables species to avoid competing for
355 very limited natural resources during winter. Provisioning reduces overwinter mortality levels in
356 resident species, removing a key population limitation and improving the physical condition of

357 surviving resident individuals the following spring (Murray et al., 2016; Norris, 1993), nullifying the
358 benefits of migration. Additionally, non-provisioned passerines may also suffer hyperpredation
359 (Courchamp et al., 2000; Roemer et al., 2001) and all significant nest predators, including corvids,
360 squirrels, rats, foxes and great spotted woodpeckers benefit from provisioning, with a concomitant
361 increased risk of nest predation demonstrated in the vicinity of food provisioning (Hanmer et al.,
362 2018, 2017). As provisioning occurs ubiquitously in the UK (Davies et al., 2012), these effects are
363 likely to be widespread, and particularly damaging to species with small populations (Roemer et al.,
364 2001), such as those declining in Fig 2.

365

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

369

370 **5. The time for a change of policy?**

371

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

380

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

389

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

396

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

405

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407

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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	<p>Providing resources to specific species which have been lost to them in the natural environment, often following disturbance.</p> <p>Examples:</p> <ul style="list-style-type: none"> • 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 <p>Motivations: conservation intervention to maintain or boost populations of threatened species</p> <p>References: Garnett et al., 1999; González et al., 2006; Olaciregui et al., 2020</p>	<p>Providing resources necessary for multiple species which have been lost in the landscape, aimed at wildlife in general.</p> <p>Examples:</p> <ul style="list-style-type: none"> • 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 <p>Motivations: conservation intervention to support ecological communities after a general loss of resources.</p> <p>References: Bolam et al., 2020; Brock et al., 2017; Cortés-Avizanda et al., 2016</p>
Additional resources	<p>Providing resources to specific species which are additional to those naturally available, often to boost populations or attract individuals.</p> <p>Examples:</p> <ul style="list-style-type: none"> • 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 <p>Motivations: attracting species to designated areas for viewing by tourists, study by researchers, or baiting for hunting. Also to boost populations of threatened species.</p> <p>References: Burgin and Hardiman, 2015; Clout et al., 2002; Selva et al., 2014; Woods et al., 2010</p>	<p>Providing resources for multiple species and communities which are additional to those naturally available.</p> <p>Examples:</p> <ul style="list-style-type: none"> • 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 <p>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.</p> <p>References: Brock et al., 2017; Cox and Gaston, 2018; Tshipa et al., 2017</p>

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	<ul style="list-style-type: none"> • Enjoyment value of wildlife interaction • Improved mental health, wellbeing and relaxation • Link to, and engagement with, nature <p>References: Brock et al., 2017; Cox and Gaston, 2018; Luck et al., 2011</p>	<ul style="list-style-type: none"> • Monetary and time costs of provisioning • Human-wildlife conflict if undesirable species are encouraged • Zoonotic disease transfer <p>References: Cox et al., 2018; Cox and Gaston, 2018; Lawson et al., 2014</p>
Effects on provisioned recipient	<ul style="list-style-type: none"> • 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 <p>References: Fuller et al., 2008; Greig et al., 2017; Plummer et al., 2019; Robb et al., 2008a; Shutt et al., 2021a; Wilcoxon et al., 2015</p>	<ul style="list-style-type: none"> • 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 <p>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</p>
Indirect ecosystem effects	<ul style="list-style-type: none"> • Increased prey for predators of recipient taxa • Enhanced environmental awareness and pro-environment behaviours of provisioners 	<ul style="list-style-type: none"> • 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

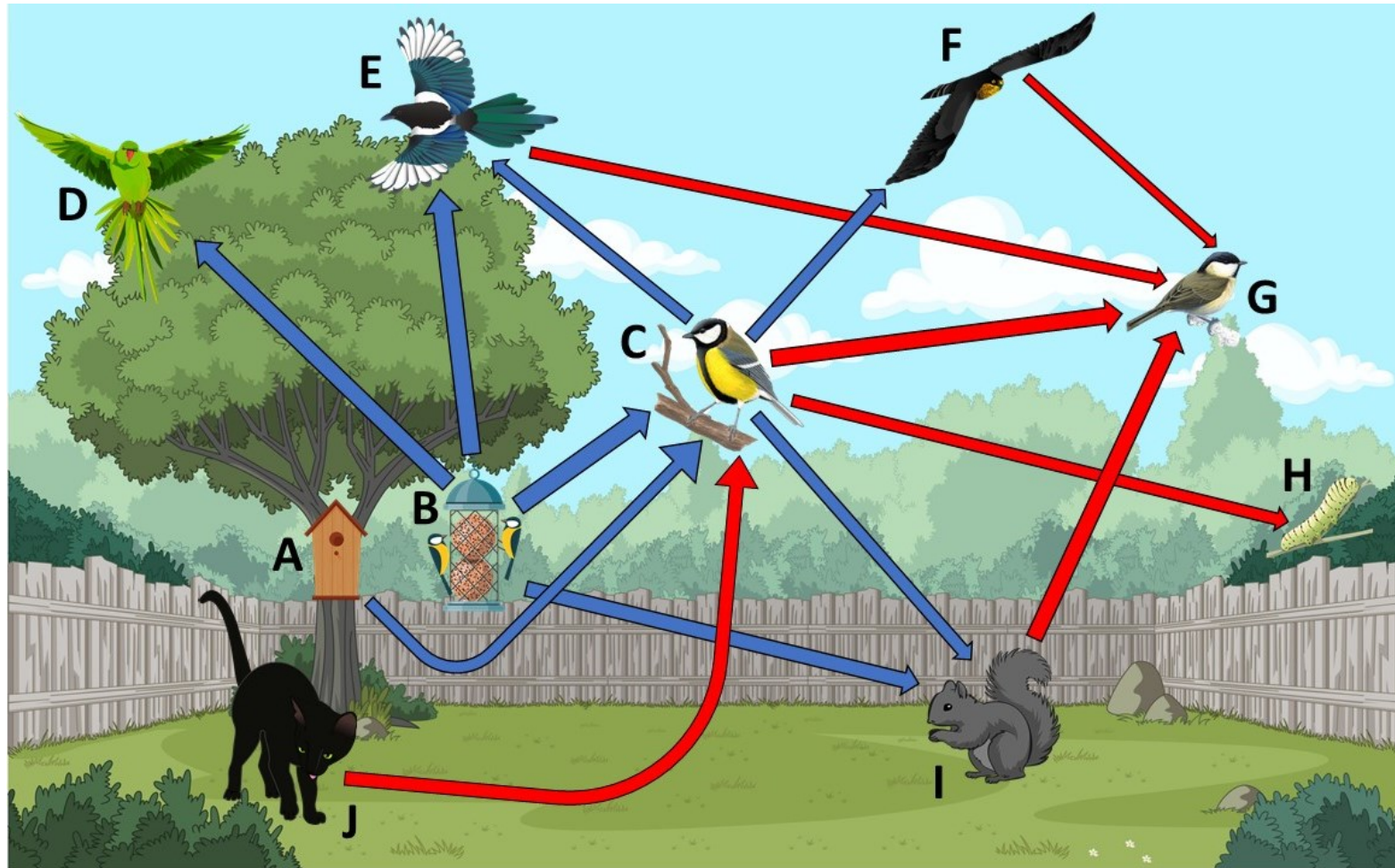


Fig 1 Schematic illustrating novel interactions facilitated by garden bird provisioning. All arrows indicate predation with the exception of the one between C and G which indicates competition. Red arrows indicate a negative effect while blue arrows indicate a positive effect. Arrow size is not indicative 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.

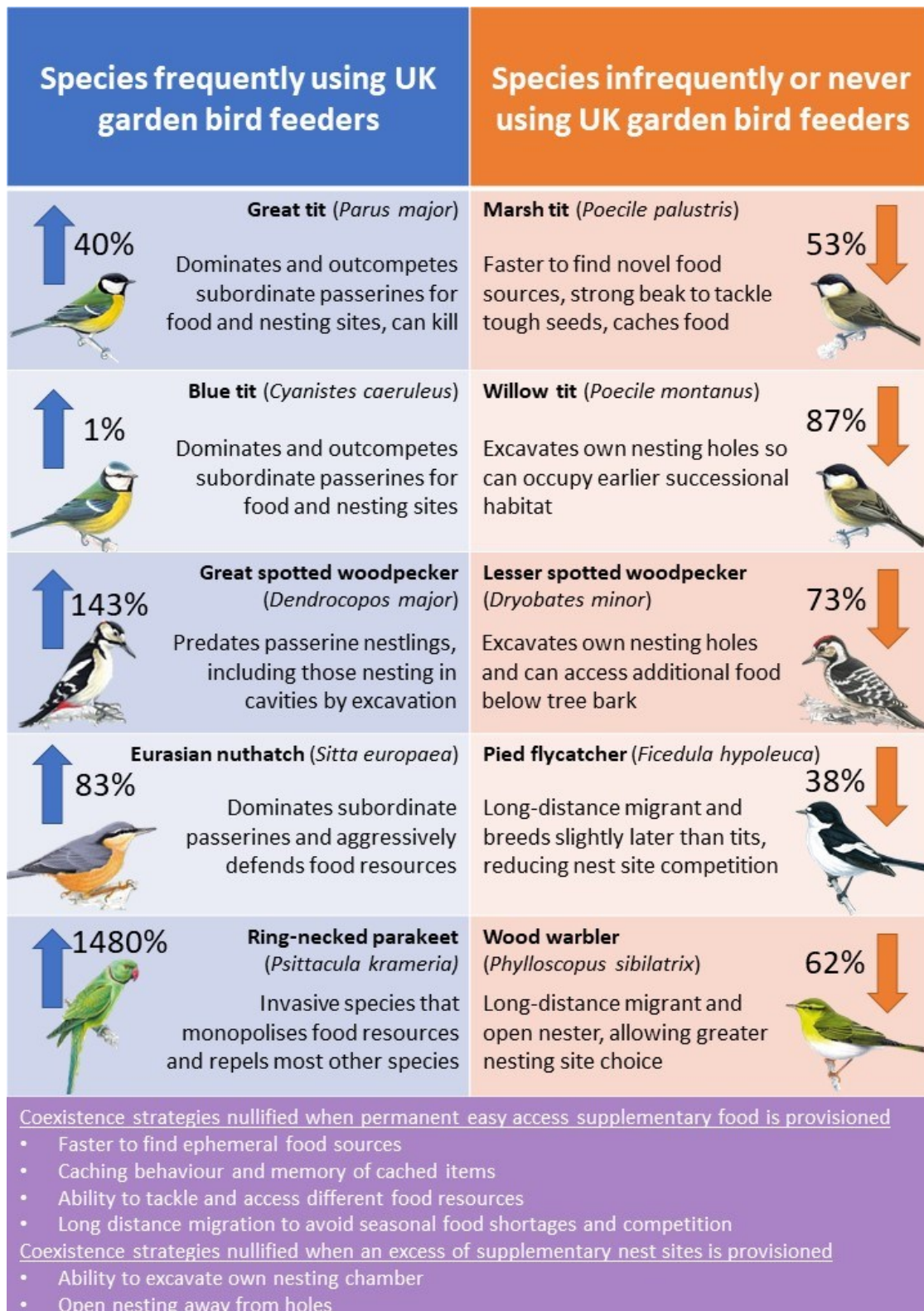
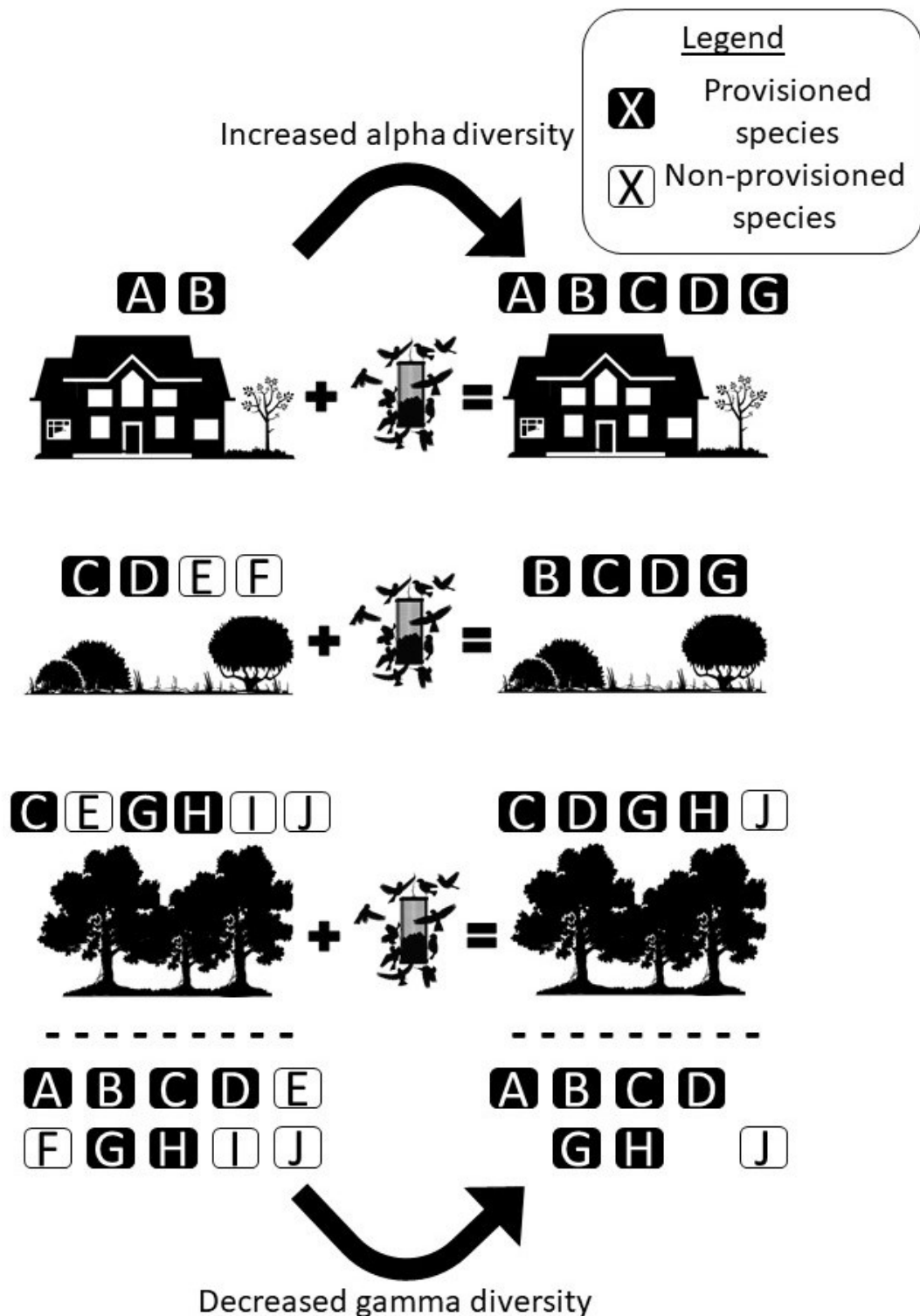


Fig 2 Representative UK woodland bird species that regularly take advantage of garden bird food provisioning (left, blue) and those that don't or only do so infrequently (right, orange). Population trends (25-year) are depicted (Massimino et al., 2019) along with traits that either facilitate outcompeting 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.