Supplementary bird feeding as an overlooked contribution to local phosphorus cycles

Andrew J Abraham[1,2*], **Christopher E Doughty**[2], **Kate E Plummer**[3,4], **and Ethan S Duvall**[5]

Supplementary feeding of garden birds and gamebirds is a common practice worldwide. Bird feed is rich in phosphorus (P), which plays a key role in animal health and ecosystem function. However, much of the P in bird feed originates from mined rock deposits, which is then transported thousands of kilometers to feeder stations, where it represents an external source of nutrients for recipient ecosystems. Here, we demonstrate that diffusion of P by birds and other animals from feeder stations to ecosystems can represent a nontrivial contribution to local biogeochemical cycles. Using the UK as a case study, we show that supplementary bird feeding supplies 2.4 (range: 1.9–3.0) gigagrams of P per year across the UK, a flux similar in magnitude to atmospheric deposition. Phosphorus provided to garden birds alone is equal to that supplied through the application of garden fertilizers. In natural and semi-natural ecosystems, additional feeder-derived P inputs may exacerbate eutrophication at the local scale and adversely impact biodiversity.

Front Ecol Environ 2024; e2793, doi:10.1002/fee.2793

Supplementary feeding of garden birds has become common practice worldwide, particularly in higher-income countries, with an estimated global market of US\$5–6 billion yr^{-1} (Jones 2018). Such practices are often used to promote human–wildlife interactions and bird welfare (Cox and Gaston 2016). Likewise, supplementary feed is liberally provided for gamebirds, such as ring-necked pheasants (*Phasianus colchicus*) and red-legged partridges (*Alectoris rufa*), where motivations are primarily focused on increasing the size and density of birds raised for harvest (Sage *et al.* 2020). While bird feeding can improve survivorship and reproduction of target species (Draycott *et al.* 2005; Robb *et al.* 2008), it can also negatively impact ecosystem stability through changes to bird community composition (Galbraith *et al.* 2015; Plummer *et al.* 2019; Sage *et al.* 2020), behavior (Clucas and Marzluff 2012), dominance hierarchies (Francis *et al.* 2018), distribution (Fuller *et al.* 2008), and transfer of avian diseases (Lawson *et al.* 2018).

In a nutshell:

- Supplementary bird feeding is a common practice worldwide; seeds, grains, and nuts provided in bird feed are rich in phosphorus (P), a key element that shapes ecosystem composition and function
- Free-ranging wildlife disperse P from bird feeding stations into local environments, fertilizing recipient ecosystems
- In the UK, P supply at bird feeding stations is similar in magnitude to important abiotic (eg atmospheric deposition) and anthropogenic (eg horticulture fertilizer) inputs
- For natural and semi-natural ecosystems, P dispersal from bird feeders may negatively impact ecosystems through cascading effects of increased P availability, such as modifying competitive advantages between species or promoting eutrophication

To date, most scientific research has focused on the direct impacts of supplemental bird feeding on wildlife populations and disease dynamics (Robb *et al.* 2008; Sage *et al.* 2020). Yet, indirect effects of bird feeding may also be pervasive and influence broader ecosystem processes (Shutt and Lees 2021). For example, the consumption and dispersal of anthropogenically sourced nutrients by wildlife may represent a major flux within local biogeochemical cycles (Abraham *et al.* 2023). Where such activities lead to eutrophication, the composition and function of nearby ecosystems may be adversely impacted (Elser *et al.* 2007; Du *et al.* 2020; Penuelas *et al.* 2020; Abraham *et al.* 2022). Despite the considerable scale of bird feed production and supply, little attention has been given to understanding the fate of nutrients in bird feed and what impact this may have for recipient ecosystems.

Provision of supplementary resources, such as bird feeding, can be targeted (eg species-specific) or generalized for multiple species, and can provide replacement or additional resources beyond those naturally available (Shutt and Lees 2021). Where bird feeding is targeted and replaces human-induced nutritional shortages (eg by helping European farmland birds through the winter “hungry gap”; Broughton *et al.* 2020), changes to biogeochemical cycles

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*[1]Centre for Biodiversity Dynamics in a Changing World and Centre for Ecological Dynamics in a Novel Biosphere, Section of EcoInformatics and Biodiversity, Department of Biology, Aarhus University, Aarhus, Denmark; [2]School of Informatics, Computing and Cyber Systems, Northern Arizona University, Flagstaff, AZ *(andrew.abraham@bio.au.dk); [3]British Trust for Ornithology, Thetford, UK; [4]Centre for Ecology and Conservation, Faculty of Science, Environment and Economy, University of Exeter, Penryn Campus, Penryn, UK; [5]Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY*

may be limited. In contrast, where provisioning occurs at high rates or over long periods, and is in addition to natural fluxes, bird feeding may represent a major external source of nutrients, with implications for ecosystem composition and function (Abraham *et al.* 2023). It is important that any changes to biogeochemical cycles caused by bird feeding be quantified to help guide sociocultural attitudes and policy positions toward this widespread practice. Here, we contextualize the magnitude of supplementary bird feeding within regional biogeochemical cycles, using the UK as a case study. Specifically, we focus on phosphorus (P), a key component of bird feed and pivotal for constraining ecosystem composition and function within the UK and globally (Elser *et al.* 2007; Du *et al.* 2020; Penuelas *et al.* 2020; Abraham *et al.* 2022).

Phosphorus and bird feed: from rocks to feeders to ecosystems

Bird feed typically consists of seeds, grains, and nuts, which contain high concentrations of fats, proteins, and biologically important nutrients such as P (Jones 2018). Feed mixes can be simple, consisting of only one or two components, or complex formulations. Feed suppliers source their raw materials from across the global market, which is subject to spatial and temporal dynamics (Lin 2005; Simoes and Hidalgo 2011). However, the US (eg wheat, peanuts), eastern Europe/Russia (eg wheat, millet, sunflower seeds), Turkey (eg hazelnuts), Brazil/Argentina (eg soy, Brazil nuts), India (eg millet, niger seeds, peanuts), and China (eg peanuts, sunflower seeds) are important providers (Lin 2005; Simoes and Hidalgo 2011). As with almost all non-organic commercial crops, the constituents of bird feed are grown with P fertilizer, which is primarily derived from mined rock deposits in Morocco, the US, China, Jordan, and South Africa (Ashley *et al.* 2011). Consequently, P supplied to wildlife via bird feed is almost always allochthonous (originating from an external environment) and is often sourced from thousands of kilometers away (Figure 1).

Supplementary food for birds is usually placed in hanging feeders or on platforms (bird tables) near people's homes for garden birds, or in hoppers spread across estates for game birds, where it attracts both target and non-target species (Sánchez-García *et al.* 2015; Jones 2018). Animals may travel considerable distances and modify their movement patterns to acquire nutritional benefits from feeder stations (Abraham *et al.* 2023). In many cases, supplementary feed contributes substantially to dietary intake, increasing the proportion of external nutrients cycled into the ecosystem. For example, in the UK, blue tit (*Cyanistes caeruleus*) individuals derive 6–26% of their food from provisioned feed (Robb *et al.* 2011). Where gamebirds are released for hunting recreation, supplementary feeding stations are used to elevate their densities beyond the local ecosystem carrying capacity (Sánchez-García and Buner 2017), and constitute a substantial component of their nutritional intake (Draycott *et al.* 2005; Sánchez-García *et al.* 2015).

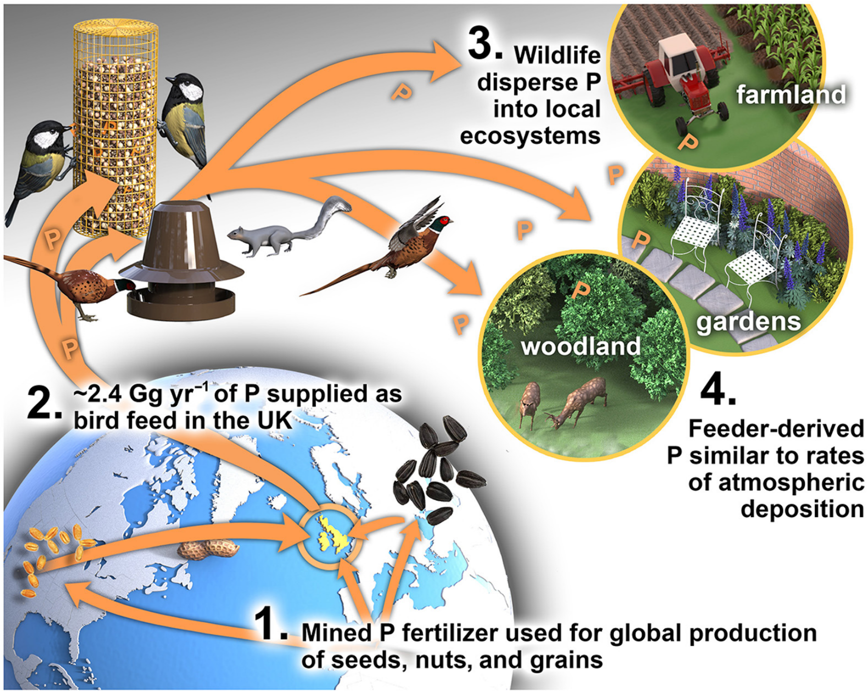

Figure 1. Phosphorus (P) is globally transported by humans from P-rich rock deposits to agricultural fields, where it is used as a fertilizer to grow seeds, nuts, and grains. These components of bird feed are then transported through the global market to feeder stations, often located thousands of kilometers away. Here, birds and other wildlife efficiently disperse P into surrounding ecosystems. Allochthonous P input into recipient landscapes by birds and other wildlife can have profound effects on ecosystem composition and function, before ultimately being exported through rivers into the ocean. Graphic credit: V Leshyk.

Due to their high metabolism and mobility, birds are markedly effective dispersal agents, as evidenced by their important roles in seed dispersal (Gaston 2022). Consequently, allochthonous P provided in supplementary feed can be dispersed into ecosystems far from feeding stations. For example, Shutt *et al.* (2021) found that supplementary feed was still found in the feces of great tits (*Parus major*) sampled at more than 1.4 km from the nearest house. Non-target taxa, including rodents, lagomorphs, and ungulates, can also consume high quantities of bird feed (Reed and Bonter 2018) and may represent a key component of nutrient dispersal in some locations. On the basis of camera trap data from 259 feeding stations provided for gamebirds in southern England, Sánchez-García *et al.* (2015) found that 67% of grain was consumed by non-target species (eg mammals), which also disperse nutrients away from feeding stations (Abraham *et al*. 2022). Migratory birds, such as the European goldfinch (*Carduelis carduelis*), have the additional potential of transporting nutrients incorporated in their bodies over hundreds of kilometers away when they die. Finally, many seeds are discarded by birds while they feed, leading to a buildup of unconsumed food in the vicinity of feeding stations. Consequently, anthropogenic P is efficiently diffused from feeder stations into local and distant environments via the excrement and bodies of a diverse variety of free-ranging wildlife.

At national scales, natural abiotic and biotic P fluxes have become dwarfed by anthropogenic transport of P via agricultural fertilizer (Abraham *et al*. 2022; Rothwell *et al*. 2022). However, human activities tend to concentrate P into nutrient hotspots within certain parts of the landscape (eg fertilized fields, landfill sites; Rothwell *et al*. 2022). In these hotspot locations, additional P inputs from bird feed will likely have negligible effects, given that these ecosystems are already saturated with P. However, animals may play an important role in transporting allochthonous P into surrounding, unfertilized environments (Abraham *et al*. 2022). For example, Winton and River (2017) calculated that gulls (Laridae spp) in North America transport ~139,000 kilograms of P per year from P-rich landfill sites to neighboring P-limited waterbodies. As wildlife often display habitat preferences, this may generate advection of nutrients into specific ecosystems (eg forest patches; Fujita and Koike 2007).

Changes to P availability in terrestrial ecosystems can have profound consequences, including cascading effects on plant, microbial, and animal competition, composition, production, and invasion (Penuelas *et al*. 2020). These effects occur by lifting growth constraints of P limitation, altering nutrient stoichiometries (nitrogen-to-phosphorus [N:P] ratios), or interfering with uptake of other important nutrients (eg nitrogen [N], calcium, zinc; Abraham *et al*. 2023). Import of allochthonous P into aquatic systems can also exacerbate localized issues of eutrophication, particularly in already P-saturated areas of the world (Withers and Jarvie 2008; Penuelas *et al*. 2020). For example, P transport by gulls to waterbodies in the above example is thought to be undermining regional P-reduction goals (Winton and River 2017). Such issues of P pollution are compounded by the fact that global P resources are finite and slowly being depleted, making it increasingly important for humans to maximize P use-efficiency (Ashley *et al*. 2011; Abraham *et al*. 2022; Rothwell *et al*. 2022).

The case of the UK

It was estimated that in 2022 more than half of all households (58%) in the UK with outdoor space provided food sources for wild birds, spending a total of £345 million, and equating to the annual supply of ~150,000 metric tons of seed mixes for garden birds (UK Pet Food 2015, 2022). Orros and Fellowes (2015) estimated that if all of this available feed was consumed by common garden birds (eg robins, tits, finches) it could support 196 million individuals, far exceeding the actual abundance of this group in the UK. Similarly, ~282,000 metric tons of wheat supplement and ~92,000 metric tons of grower pellets are provided annually for ~43 million gamebirds, predominately ring-necked pheasants and red-legged partridges released for harvest (Madden 2021; Harris 2021). A gamekeeper's conservation and wildlife survey found that >85% of shooting estates provide supplementary feed, with annual provision ranging from 0.5 to 3000 metric tons (Ewald and Gibbs 2020).

To calculate P supply in bird feed across the UK, we collated data on the supply and P concentration of commonly provided feed items (see Appendix S1: Panel S1, Tables S1–S4). However, detailed information (eg quantities or components of specific seed mixes) was unavailable at the national scale. We therefore obtained an average P concentration for three broad diet categories for which quantities are known, consisting of seed mixes, wheat supplement, and grower pellets. We generated uncertainty bounds around these averages using minimum and maximum values for each category. Mean P concentration by mass was lowest in wheat supplement (0.35%; range 0.28–0.42%), intermediate in bird seed mixes (0.48%; range 0.28–0.66%), and highest in grower pellets (0.74%; range 0.65–0.85%). Using Equation 1, where M is the mass of bird feed provided in the UK and C is P concentration from Appendix S1: Tables S2–S4, we estimated total P supply in bird feed equal to 2.4 (range: 1.9–3.0) gigagrams of P per year (Gg P yr^{-1}):

$$P_{\text{bird\_feed}} = \sum \left(M_{\text{seed}} \times C_{\text{seed}}\right) + \left(M_{\text{wheat}} \times C_{\text{wheat}}\right) + \left(M_{\text{pellets}} \times C_{\text{pellets}}\right) \qquad \text{(Equation 1).}$$

Due to issues of P pollution in the UK, much effort has been recently dedicated toward the accounting of P fluxes nationally (eg Cooper and Carliell-Marquet 2013; Rothwell *et al*. 2022). A recent flow analysis by Rothwell *et al*. (2022) found that the UK's P budget is largely driven by imported fertilizer for agriculture (82.6 Gg P yr^{-1}) and feed for domestic livestock (45.0 Gg P yr^{-1}). Accordingly, at the national scale, we find the P flux in supplementary bird feed (2.4 Gg P yr^{-1}; Figure 2a) to be of second-order importance as compared to these primary fluxes, yet of a similar magnitude to the P flux of imported crop seeds for agriculture. Consequently, P transported from bird feeders to production landscapes for crops and livestock in the UK likely has small effects. Indeed, in these environments, birds are more likely a net sink of P due to the consumption of P-rich agricultural seeds and crops (Wilson *et al*. 1996).

However, comparing the national supply of P in bird feed to abiotic and anthropogenic P fluxes considered important for semi-natural systems in the UK (eg woodlands, grasslands, moors, heathlands, aquatic systems) indicates that supplemental

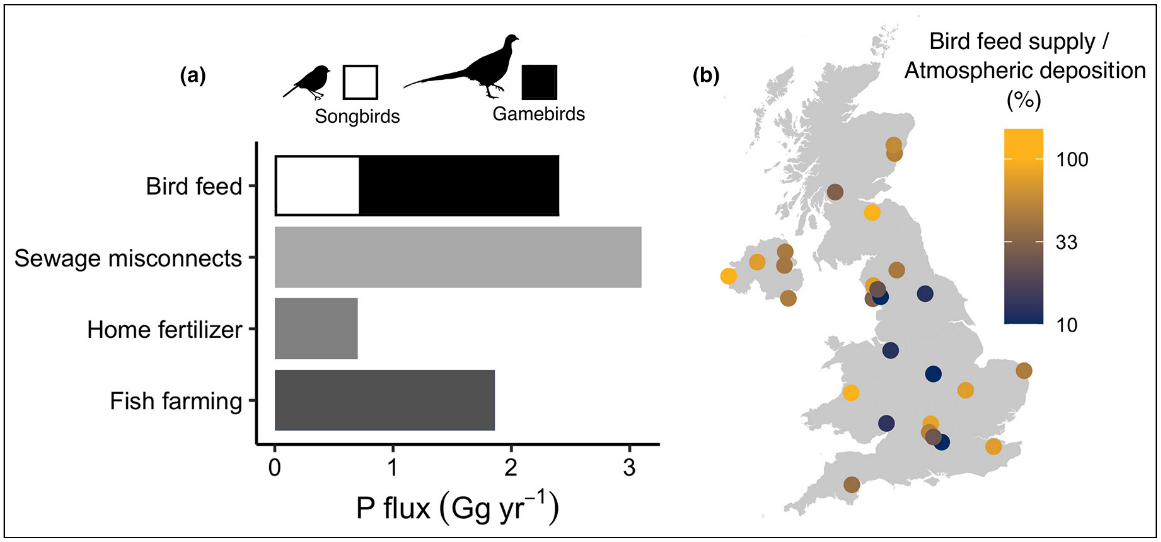

Figure 2. Comparison of our "best" estimate of P provisioning in supplementary bird feed to (a) three select P fluxes in the UK (sewage misconnects, non-agricultural [home] fertilizer, and fish farming) from Rothwell *et al.* (2022) and (b) atmospheric P deposition for 28 sites from Tipping *et al.* (2014). In panel (b), we assumed that bird feed input is equally distributed across the UK with values presented as a percentage, where points above or below 100 indicate bird feed flux greater than or less than atmospheric flux, respectively. Note that the color bar is $\log_{10}$ scaled.

bird feeding may be important for these environments. For example, even our conservative lower estimates are over twice (2.8 times) that of the permitted discharge of P from industrial food processing to natural waterbodies (Rothwell *et al.* 2022). If we use our "best" estimate and assume that P input from bird feed is equally dispersed across the UK, this represents a flux equal to ~0.01 grams per square meter per year, which is on average 55% (range: 8–163%) of atmospheric deposition measured at 28 sites (Figure 2b; Tipping *et al.* 2014), an important flux for many semi-natural environments (Elser *et al.* 2007). If the true value is closer to our upper uncertainty estimate, then the P flux from bird feeding is similar in magnitude to the P flux from sewage misconnects (ie incorrectly connected wastewater that ends up in surface drainage rather than the sewer network) (3.1 Gg P yr^{-1}; Rothwell *et al.* 2022), which has been subject to scrutiny in the UK due to issues of pollution and eutrophication (Withers and Jarvie 2008; Comber *et al.* 2013). Consequently, allochthonous P from bird feed is likely a nontrivial flux entering these landscapes at the national scale.

In reality, the transport of P from feeder stations by wildlife will be heterogeneous in time and space, with some areas receiving higher deposition rates than others. Areas with greater densities of supplementary feeding stations (eg near shooting estates or residential areas; Davies *et al.* 2012) or sites of high wildlife congregation (eg forest patches; Fujita and Koike 2007) may receive considerably higher P inputs. By contrast, mountainous areas (eg the Scottish Highlands), where bird feeding occurs at lower densities, are predicted to have smaller inputs. Future work should assess which geographic areas and habitat types are most vulnerable to additional P subsidies via the bird feed pathway. For instance, we show that P supply for garden birds (songbirds) (~0.7 Gg P yr^{-1}) is approximately the same as that used for non-agricultural (home) fertilizer (0.7 Gg P yr^{-1}; Figure 2a), yet there is considerable overlap between landscapes of amenity horticulture (eg gardening) and the location of supplementary feeding stations for garden birds (Davies *et al.* 2012). As a result, species like the European robin (*Erithacus rubecula*), common blackbird (*Turdus merula*), and blue tit may represent a flux of P to public parks and residential gardens at a rate similar to direct fertilizer use. Likewise, it will be important to disentangle the impacts of gamebird provisioning in woodland and farmland systems, which may attract different wildlife communities and have disparate impacts based on relative background P availability.

Where P input from bird feeding is substantial, effects on semi-natural ecosystems in the UK may be profound. For example, plant growth of herbaceous species common in old broadleaved woodlands was found to increase variably in response to P addition experiments (Hipps *et al.* 2005). Due to the competitive advantages of different (including invasive) species, plant community composition may therefore become modified under altered nutrient regimes. For instance, on the basis of 501 grassland plots in northwestern Europe (including the UK), Ceulemans *et al.* (2014) found that biodiversity is strongly constrained by P availability, with total plant species richness negatively related to soil P concentration. Consequently, where excessive, P inputs from supplementary bird feed could reduce overall plant biodiversity and contribute to the loss of endangered species (Wassen *et al.* 2005). However, it is important to note that much of the UK is considered co-limited by N and P (Du *et al.* 2020). Ecosystem effects due to additional P inputs from bird feeding will not occur in isolation from other nutrients, and synergistic constraints between many nutrients will modulate any consequences of P nutrient enrichment (Fay *et al.* 2015).

It is even possible that P inputs from supplementary bird feed may help rebalance anthropogenic shifts in biospheric N:P ratios. Release of N by human activities (eg the Haber–Bosch process, which converts atmospheric N into ammonia) has outstripped anthropogenic changes to the P cycle, resulting in imbalances between these two nutrients (Penuelas *et al*. 2020). Allochthonous P inputs from wildlife may act to rectify local disparities, albeit with higher total nutrient concentrations and associated ecological consequences. Further research is needed to examine such possible effects.

Additional P inputs from bird feed will not remain in ecosystems indefinitely. Instead, excess P is eventually exported into freshwater systems, which can cause eutrophication (Withers and Jarvie 2008). Nationally, the P flux into rivers is dominated by agricultural run-off and sewage effluent (Cooper and Carliell-Marquet 2013; Rothwell *et al*. 2022). However, there may be sites where P pollution from supplementary bird feed is important (eg headwater streams in areas where gamebird feeding is high; Withers and Jarvie 2008). Ultimately, P derived from supplementary bird feed will eventually enter nearshore marine ecosystems, with potentially harmful effects. For example, direct anthropogenic inputs of P into nearshore marine environments for finfish farming (1.9 Gg P yr^{-1}) are known to contribute to nutrient pollution (Rothwell *et al*. 2022). We show here that, at the national scale, the P flux in supplementary bird feed (~2.4 Gg P yr^{-1}) is ~1.3 times that of the P flux in fish farming (1.9 Gg P yr^{-1}), although we recognize that this comparison overlooks differences in the characteristics of P supply, such as being a concentrated (ie fish farming) versus dispersed (ie bird feeding) source (Figure 2a).

Perspectives and implications

The fertilization of landscapes by birds has long been recognized. Guano (bird excrement) has been used by Indigenous groups to amend soil fertility in South America for well over 1500 years, and 18th- and 19th-century merchants transported vast quantities across the oceans to agricultural fields in Europe and North America (Ashley *et al*. 2011). Today, commercial mining of guano has given way to P extraction from mined rock deposits (Ashley *et al*. 2011; Abraham *et al*. 2022). Yet, via the ubiquitous provision of supplementary seeds, grains, and nuts for garden birds and gamebirds, humans continue to link local P dispersal by birds with global anthropogenic transport (Figure 1). Through the combined magnitude of provisioned bird feed, high nutritional content, elevated animal densities, and high dispersal capacity of wildlife, supplementary bird feeding may profoundly contribute to local biogeochemical cycles, with likely implications for biodiversity, ecosystem functioning, and sustainability of natural and semi-natural landscapes.

It is important to consider the fate of nutrients from supplementary bird feed, as supply—already a multi-billion-dollar industry—is increasing over time (Jones 2018). New products for feeding garden birds are being marketed to consumers at an exponential rate (Figure 3a; Plummer *et al*. 2019), while the global bird food market, which includes food for wild and caged pet birds, is estimated to increase at a compound annual growth rate of 3.6%, from US$2.1 billion in 2022 to US$3.0 billion by 2032 (Figure 3b; FMI 2023). Notably, supplementary bird feeding is also increasing rapidly in low-income countries, particularly in Asia and South America, that previously did not engage extensively in this practice (Figure 3c; Alexandrino *et al*. 2022; FMI 2023). Although the impacts of bird feeding vary geographically and depend on various biotic (eg wildlife composition) and abiotic (eg specific nutrient constraints; Fay *et al*. 2015; Du *et al*. 2020) factors, the presented case study of the UK should serve as a cautionary example for other countries. Yet supplementary feeding of garden birds is widely supported by many nongovernmental organizations and government agencies worldwide (Jones 2018; Baverstock *et al*. 2019), while supplementary feeding of gamebirds is promoted by gamekeeper organizations (Sánchez-García and Buner 2017; Ewald and Gibbs 2020; Harris 2021).

In some cases, supplementary feeding can positively facilitate human–wildlife interaction or aid in attaining conservation/management goals without substantial impact on overall ecosystem integrity (Cox and Gaston 2016; Broughton

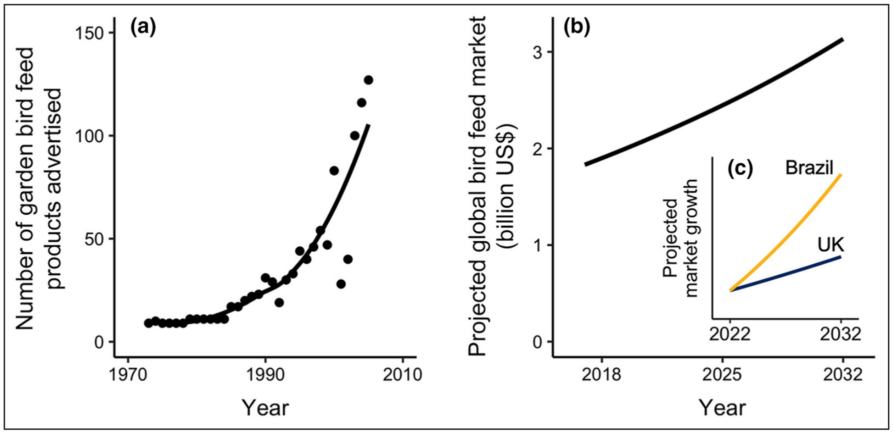

Figure 3. (a) Changes in UK garden feeding products over time, adapted from Figure 1 in Plummer *et al*. (2019); (b) projected global bird feed market value in billions of US dollars for the period 2017–2032 (data from FMI [2023]); and (c) projected changes in spending on bird feed products for (i) a country with a long history of wild-bird feeding (eg UK; compound annual growth rate = 1.5%) and (ii) a country with a developing history of wild-bird feeding (eg Brazil; compound annual growth rate = 4.5%) over the period 2022–2032 (data from FMI [2023]). In panel (a), the line depicts the temporal trend in various types of bird foods (circles) advertised in *Birds* magazine of the Royal Society for the Protection of Birds.

et al. 2020; Sage *et al.* 2020). However, a substantial body of literature demonstrates that, in many places, the magnitude of current provisioning generates numerous unintended consequences, such as changes in bird community composition, behavior, and disease spread (Robb *et al.* 2008; Lawson *et al.* 2018; Sage *et al.* 2020; Broughton *et al.* 2021; Shutt and Lees 2021). We believe that bird feeding may also have unconsidered repercussions for broader ecosystem dynamics, including biogeochemical cycling. Additional research is needed to better quantify the magnitude of nutrient inputs from bird feeding at local scales, identify areas subject to high levels of nutrient deposition by wildlife, and evaluate ecosystem responses to altered supplementary bird feed regimes. In the meantime, we support the salient advice of Broughton *et al.* (2021), who highlighted the need to invoke the "precautionary principle" and where possible reconsider and reduce regular bird feeding.

Acknowledgements

We thank S Rothwell for sharing information on phosphorus fluxes in the UK. Our thanks are also extended to J Trepel, U Gélin, C Mare, and E Brandt for helpful comments on earlier versions of the manuscript. AJA was supported by Horizon Europe Marie Skłodowska-Curie Actions grant agreement #101062339; ESD was supported by the Cornell Atkinson Center for Sustainability's Sustainable Biodiversity Fund and the Athena Fund for Research at the Cornell Lab of Ornithology.

Data Availability Statement

No data were collected for this study.

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