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RESEARCH ARTICLE

Nutrient fertilization by dogs in peri-urban ecosystems

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Abstract

1. (Semi-)natural ecosystems provide many important benefits to nature and people, but are often located near populated and urbanized areas across the globe. During recreational activities, many people bring dogs into peri-urban forests and nature, but their nutrient inputs per unit space and time via dog faeces and urine into ecosystems remain scarcely quantified.
2. Here, we estimate net fertilization rates of dogs in peri-urban ecosystems, with a focus on nitrogen (N) and phosphorus (P) because of their evident effects on plant biodiversity. We used 487 direct-count censuses over 1.5 years to collect accurate dog abundance data per hectare per year in four sites in peri-urban forests and nature reserves in Belgium. Based on estimated dog densities and a systematic literature search of nutrient concentrations in urine and faeces, we calculate N and P fertilization rates from urine and faeces deposits, also propagating uncertainty and variability in these estimates.
3. We find that canine N and P fertilization rates on average amount to 11 kg N (more or less equally from urine and faeces) and 5 kg P (predominantly from faeces) per hectare per year, respectively. These estimated amounts are substantial when compared to atmospheric inputs of N and extractable amounts via traditional nature management (e.g. mowing and hay removal).
4. Our estimated dog N and P fertilization rates in peri-urban forests and nature are substantial. Such levels of nutrient inputs may considerably influence biodiversity and ecosystem functioning, and co-determine restoration outcomes. Our results underpin the need for managers and policy makers to more often (i) consider currently neglected nutrient inputs by dogs in management plans and restoration goals, (ii) communicate to dog walkers the role of their dog as 'fertilizer' and highlight the necessity to remove at least canine solid faecal waste, (iii) in sensitive oligotrophic ecosystems with species adapted to nutrient-poor soils, establish nearby off-leash dog parks, enforce the use of short leashes and/or apply dog bans such that high dog abundances can be avoided.

KEYWORDS
biodiversity loss, *Canis familiaris*, eutrophication, fertilization, forest and nature management, nitrogen deposition, nutrient enrichment, peri-urban ecosystems, phosphorus, recreation

1 | INTRODUCTION

Peri-urban ecosystems such as forests, (semi-)natural grasslands, wetlands and heathlands in populated areas across the globe provide many important benefits to nature and people such as biodiversity conservation, carbon drawdown, nutrient cycling, climate regulation, wood and food production and recreation (Perring et al., 2013). In many instances, such ecosystems are on the one hand of important conservation concern, but on the other hand also experience significant amounts of daily human visitors, especially when located near relatively densely populated and urbanized areas. The impacts of human recreationists on disturbance of wildlife such as breeding birds are relatively well-quantified (Arnesen, 1999; Lenth et al., 2008). However, many people also bring domestic dogs (*Canis familiaris*) on recreational activities. While effects of dogs on wildlife via direct mortality, disturbance and disease transmission have been relatively well documented, their fertilization effects have received considerably less attention (Weston et al., 2014).

There are an estimated 87 million dogs in Europe and 72 million in the United States (FEDIAF, 2019; Paradeis et al., 2013). In Europe and the United States, about 25% and 49% of households owns at least one dog, respectively (Allen et al., 2020; FEDIAF, 2019). Via their urine and solid waste (faeces), dogs bring in significant amounts of nutrients into ecosystems but this disturbance and its associated effects on biodiversity have been often neglected so far. Dog faeces and urine count as net inputs, because dogs are fed at home with a protein-rich diet, in contrast to grazing cattle (*Bos taurus* L.), sheep (*Ovis aries* L.) or foraging birds that feed off the land and recycle nutrients within the ecosystem. While several studies have detected significantly elevated soil nutrient concentrations in areas with many dogs (Allen et al., 2020; Bonner & Agnew, 1983; Oates et al., 2017; Paradeis et al., 2013), dog fertilization rates per unit time and space (kg per ha per year), however, have not been quantified at the ecosystem level such that management actions with regard to dogs tend to only focus on their effects on wildlife.

Nutrient inputs from canine urine and faeces can have important effects on soil nutrient concentrations, particularly in terms of the macronutrients nitrogen (N) and phosphorus (P). In areas with a lot of dog walkers, and especially near walking paths, elevated soil P and N concentrations are found and stable isotope analyses confirmed dogs as the source (Allen et al., 2020; Bonner & Agnew, 1983). These patterns were still apparent even 3 years after an imposed dog ban (Bonner & Agnew, 1983). Paradeis et al. (2013) also detected strong soil nutrient and pH impacts of dog urine within off-leash dog parks. Finally, also on marine recreational beaches, dog faeces can result in significant nutrient inputs and marine pollution (Oates et al., 2017). Elevated N and P inputs have been shown to strongly negatively impact biodiversity and ecosystem function (Bobbink et al., 2010). In plant communities, for instance, N addition decreases species richness in a wide range of ecosystems (De Schrijver et al., 2011), whereas P fertilization eradicates the niche of many threatened species (Wassen et al., 2021). In many ecosystems, also in populated areas, forest and nature management is specifically directed towards lowering soil nutrient concentrations via practices such as mowing with hay removal, local topsoil removal and phytoextraction (sometimes also referred to as mining) (Pegtel et al., 1996; Schelfhout et al., 2015, 2017, 2019). Neglecting the nutrient inputs from dogs in such cases might result in an underestimation of the time needed for ecological restoration and the costs involved. Misinformed restoration advice might negatively affect biodiversity and the associated ecosystem services.

Here, we quantified N and P inputs from canine urine and faeces in peri-urban forests and nature reserves specifically managed for biodiversity conservation and consisting of small forest patches, wetlands and grasslands with vulnerable, species-rich vegetation. Innovative to our approach is that we used nearly 500 dog density transect counts across a time span of 1.5 years to estimate N and P inputs. Combined with a systematic review of dog urine and faeces N and P concentrations, this approach enabled us to calculate dog densities and fertilization rates from both urine and faeces per unit space and time across the peri-urban ecosystems.

2 | METHODS

2.1 | Study area

This study was conducted near Ghent, a medium-sized city (about 260,000 inhabitants) in Belgium with a temperate climate (mean annual temperature of 10.3°C and mean annual precipitation of 789 mm between 1970 and 2000; Fick & Hijmans, 2017). Atmospheric N deposition was 22.7 kg N ha^{-1} year^{-1} in 2019 in the study area (Flemish Environmental Agency, 2020). We selected four study sites in peri-urban nature reserves less than 5 km from the city centre (Figure 1). The study sites are popular for recreation but also hold important biodiversity values. The study sites differ in size, in vegetation type, in management and in accessibility (Table 1), with visitors in study sites 1, 2 and 3 restricted to trails but without physical boundary to the vegetation and with visitors in site 4 legally permitted to leave the trails and walk freely in the reserve. All study sites are part of larger nature reserves and were delineated based on the physical ability of dogs to enter when off leash (borders of the study sites were often demarcated by rivers, fences or roads).

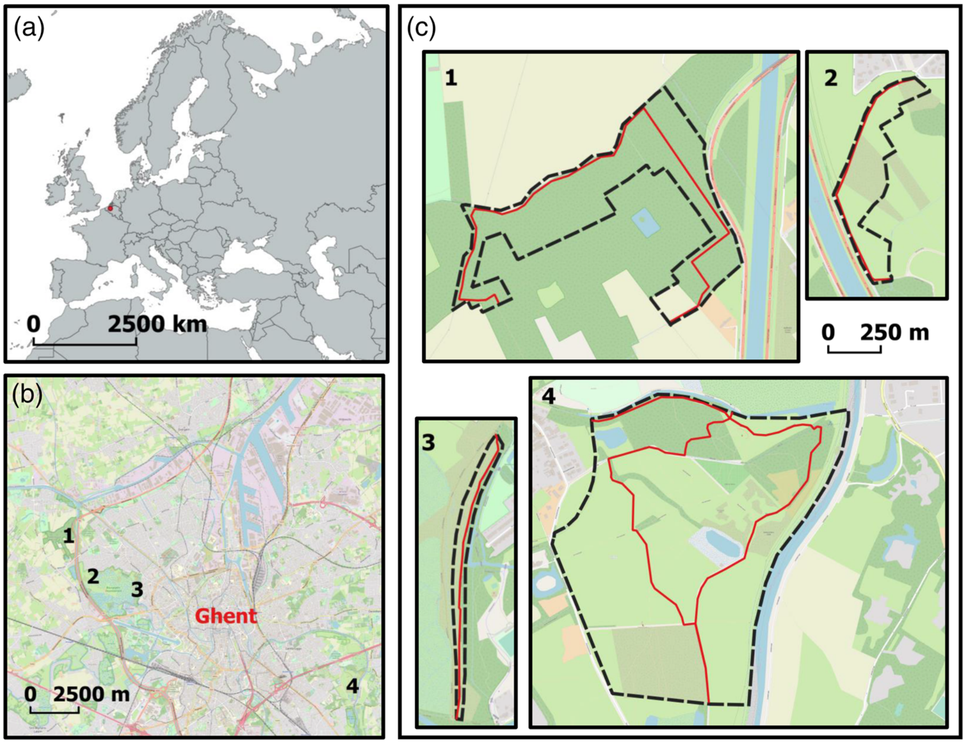

FIGURE 1 Study area. (a) Location of Ghent, Belgium in Europe (red circle). (b) Location of the four study sites around the city centre of Ghent. Numbers of sites (1-4) also refer to Table 1. (c) Detailed map of the four study sites (black dashed lines) and the covered direct count transects (red line)

TABLE 1 Overview of the characteristics of the four study sites: Location (numbers refer to the map in Figure 1), area, dominant vegetation type, management and access

Study site	Location (latitude, longitude)	Area (ha)	Dominant vegetation type (with Natura 2000 code)	Current management	Access restricted to
1. Vinderhoutse Bossen	51.08°N, 3.65°E	18.4	Alluvial forest (H91E0)	No intervention management	Paths
2. Meerskant, Bourgoyen	51.07°N, 3.66°E	5.9	Calthion grassland (H6410)	Mowing with hay removal	Paths
3. Spoorwegberm, Bourgoyen	51.06°N, 3.68°E	3.3	Lowland hay meadow (H6510)	Mowing with hay removal	Paths
4. Gentbrugse Meersen	51.04°N, 3.79°E	49.4	Oak-hornbeam-forest (H9160) and lowland hay meadow (H6510)	Low-density livestock grazing	Entirely accessible, no need to stay on paths

2.2 | Dog counts

Dogs were counted along transects in the four study sites between February 2020 and June 2021 for a total of 487 censuses. We followed a modified direct-count census to accurately and representatively quantify dog presence in each reserve (Oates et al., 2017). The transects were laid out in a way that the whole study site could be inspected when the transect was covered. A single observer per study area recorded all unique dogs on and off-leash (recorded separately) while covering the transect at a constant speed. By accounting for the size of the study site and by assuming a mean presence of the dogs of 1 h in the larger study sites 1 and 4, and of half an hour in the smaller study sites 2 and 3 and a mean daylength of 12 h, the data of every census were expressed as a number of dogs per ha per day (cf. Oates et al., 2017). Transect counts were executed two to four times weekly in each site, regardless of weather and at varying times throughout the day. In total, 487 counting events took place, more or less spread throughout the week: 46 counts on Mondays, 66 on Tuesdays, 76 on Wednesdays, 82 on Thursdays, 71 on Fridays, 61 on Saturdays and 85 on Sundays. No permission was needed for this fieldwork.

2.3 | Nutrients in urine and faeces

For the nutrient concentrations of canine urine and faeces, we performed a systematic literature search and used the mean and variation across the primary studies (Table S1). We searched for studies in Web of Science using the keywords ‘dogs and (phosph* or nitrogen) and (digestib* or excretion) and (urinary or f?ecal)' in early Nov. 2021. This search resulted in 180 potentially suitable studies. Those 180 papers were then manually screened for studies that met the following criteria: (i) N and/or P concentrations of dog urine and/or faeces were reported or could be calculated from available data; (ii) if treatments of diets or diseases were reported, we only included the control treatments and diets that could be considered as common practice. Nutrient concentrations were obtained either (i) directly if the concentrations were mentioned in the original papers or (ii) if digestibility of N (or crude protein) or P was reported, faecal concentrations were calculated based on food intake, dry matter concentration in the diet, dry matter concentration of the faeces, dietary N or P concentrations and digestibility coefficients, according to the principle of apparent digestibility calculations: Digestibility of N (or P) (%) = 100 − 100 × [(faeces (g) × faeces N (or P) concentration (g/kg)) / (food (g) × food N (or P) concentration (g/kg))]. Finally, faecal N concentrations were based on 19 diets from six studies (Beynen et al., 2002; Cargo-Froom et al., 2019; De Smet et al., 1999; Forster et al., 2012; Pinna et al., 2018; Wood et al., 2004), whereas faecal P concentrations were based on 17 diets from five studies (the same, except Forster et al., 2012). Urinary N concentrations were based on two studies (Beynen et al., 2002; Castrillo et al., 2001), whereas urinary P concentrations were based on 10 diets from three studies (Atwal et al., 2021; Stevenson et al., 2003; Wood et al., 2004), including one very well-documented study (Atwal et al., 2021).

Because dogs are carnivores and mainly fed with a protein-rich diet, the nutrient concentrations in urine are relatively high. Urine N and P concentrations amount on average to 18.7 g N L^{-1} and to 484.6 mg P L^{-1} (Table S1). Cattle urine, for comparison, has typical N concentrations of 0.7–10.2 g N L^{-1} (Hoogendoorn et al., 2010). We adopt canine faecal concentrations of 44.3 mg N g^{-1} faecal dry mass and 32.0 mg P g^{-1} faecal dry mass (Table S1). These concentrations are, again for comparison, higher than N and P concentrations of 10–30 mg N g^{-1} and 1–4 mg P g^{-1} reported for savanna ruminants (Sitters et al., 2014) and P concentrations of cattle, deer and sheep dung which ranges between 5.5 and 8 mg P g^{-1} (McDowell & Stewart, 2005). For solid waste (faeces), we assume that each dog produces faeces once on each trip with a mean dry scat weight of 100 g (de Molenaar & Jonkers, 1993). For urine, we assume that each dog deposits one quarter of the daily 736 ml urine volume production per day (Beaver, 1999; Paradeis et al., 2013) during a walk to a dog park, and thus that 184 ml urine is deposited per dog walk in the nature reserves.

2.4 | Data analyses

2.4.1 | Nutrient deposition modelling

We estimated the annual deposition of N and P through urine and faeces with an intercept-only mixed-effect model using the *lme*-function from the *nlme*-library (Pinheiro et al., 2021) with the day (numeric, counting the days from the first measurement) and site (four levels) as random-effect terms and including a temporal autocorrelation term, with a continuous time covariate. The hierarchical nature of our data and the repeated measurements within each site (time series) was hence taken into account.

Second, since there are several factors that can lead to overestimation or underestimation of our inferred fertilization rates (e.g. variation in nutrient concentrations as a result of dog food quality and quantity, imperfect detection of dogs during transect census counts, the amount of urine or faeces deposited as dependent on dog size, walk duration, dog size distribution and faeces collection rates), we also propagated uncertainty and variability on parameters as a second step. Therefore, we resampled 999 bootstrap samples from the 487 censuses in the different study sites and implemented the estimated mean and standard deviation from the nutrient concentrations obtained in the literature review (Table S1). For the parameter values for which no literature estimates were available (urine volume, faeces mass and dog residence time), we calculated the standard deviation as a value of 20% of the mean to obtain a normal distribution of estimates. For these bootstrapped estimates of the total N and P inputs per ha per year, we then report the mean and 5 and 95 percentiles of the distribution. The variability in the model parameters is shown in Figure S1. All data analyses were executed in R version 4.0.4 (R Core Team, 2021) and graphs produced with the ggplot2-library (Wickham, 2016).

2.5 | Scenario analysis

To investigate the effect of dog owner behaviour on N and P deposition, we also modelled the effect of owners keeping all dogs on a short leash (2 m) and collecting all solid faecal waste (not possible with urine), as actually prescribed by the current legislations in the different nature reserves (note there is no legal limit to leash length). If all dogs are kept on a leash of 2 m, the area of the fertilized zone is strongly reduced for study site 1 (reduced to 0.744 ha), study site 2 (0.317 ha) and study site 3 (0.348 ha). In this scenario analysis, we did not consider study site 4, because visitors there are legally permitted to leave the trails and are allowed to roam freely with dogs on a leash; the disturbed area thus remained the same.

3 | RESULTS

3.1 | Dog densities

Across the four study sites and 487 count events, we counted 1629 dogs. We calculate a mean dog density of 1.3 dogs ha^{-1} day^{-1} off leash and a mean of 2.9 dogs ha^{-1} day^{-1} on leash for a total estimated dog density of 4.2 dogs ha^{-1} day^{-1} (Figure 2). This is the equivalent of 1530 dogs ha^{-1} $year^{-1}$. There was significant among-site variation in dog densities as well as in leash use. Dog densities were highest at site 3 (which has a nature target value as species-rich grassland) where we counted a mean dog density of not less than 11.0 dogs ha^{-1} day^{-1}. Overall, 66% of encountered dogs was on leash and 34% off leash. [Correction added on 7 February 2022 after first online publication: percentages have been updated from 68% and 32% to 66% and 34%.] Yet, the proportion of off-leash dogs strongly varied among reserves

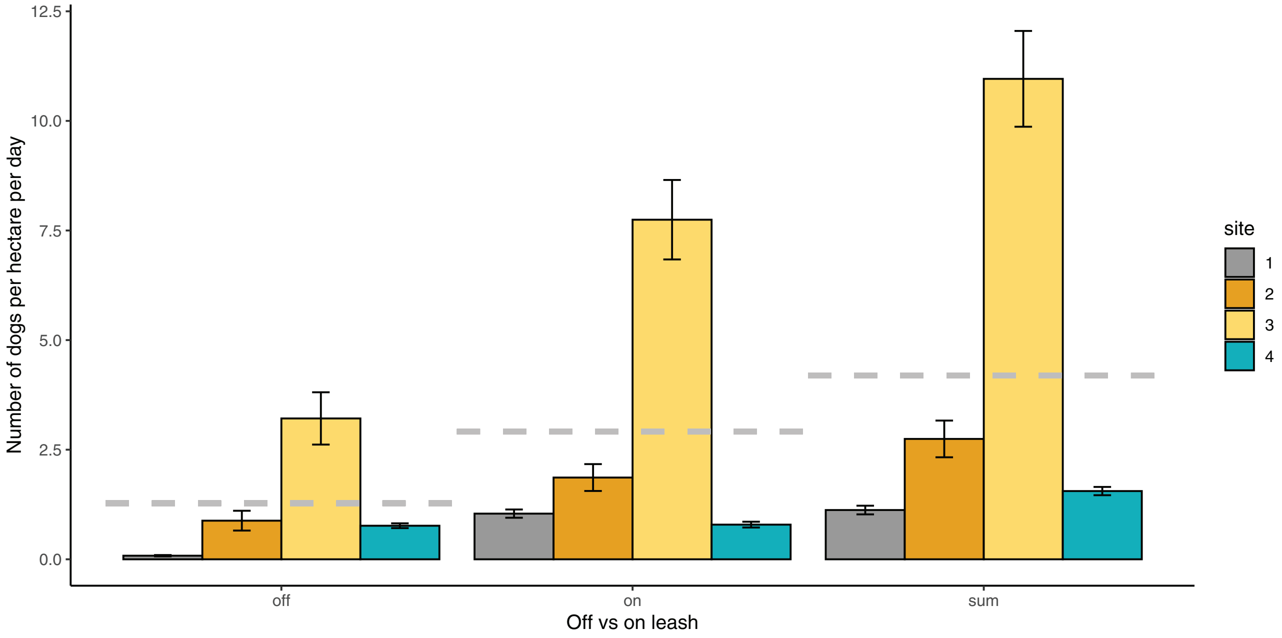

FIGURE 2 Estimated dog densities (number ha^{-1} day^{-1}), off and on leash, and their summed contributions, across the four study sites. Error bars denote standard errors. The grey dashed lines represent the mean across the four study sites

(most probably as a result of different management, policies and enforcement), from merely 8% in site 1 to 29%–49% in the other sites (Figure 2). [Correction added on 7 February 2022 after first online publication: percentages have been updated from 9% and 27%–52% to 8% and 29%–49%.]

3.2 | Estimated annual fertilization rates

Based on the estimated dog densities and intercept-only mixed-effect modelling considering temporal autocorrelation, we estimate overall N and P inputs from faeces to amount to 6.5 ± 3.7 kg N ha^{-1} year^{-1} and 4.7 ± 2.7 kg P ha^{-1} year^{-1}, respectively. Urine-based inputs of N and P amounted to 5.0 ± 2.9 kg N ha^{-1} year^{-1} and 0.13 ± 0.07 kg P ha^{-1} year^{-1}. The estimated total input of N and P across the four study sites is then 11.5 ± 6.5 kg N ha^{-1} year^{-1} and 4.8 ± 2.7 kg P ha^{-1} year^{-1}. There was again significant among-site variation driven by the variation in estimated dog densities with maximum inputs of 31.3 kg N ha^{-1} year^{-1} and 13.1 kg P ha^{-1} year^{-1} at site 3 (Figure 3).

3.3 | Scenario analysis: What if all dogs are on leash and faeces is removed

Finally, we analysed a scenario in which all detected dogs are on leashes of maximum 2 m length (excluding study site 4, cf. Section 2). Nutrients are then deposited in a significantly smaller area and concentrated in the near vicinity of the trails. This then leads to N and P deposition values of 175.3 ± 63.5 kg N ha^{-1} year^{-1} and 73.2 ± 26.5 kg P ha^{-1} year^{-1} within a zone 2 m left and 2 m right of each path (values again estimated from intercept-only mixed-effect models). If the faeces would be removed using, for example, disposal bags, urine-only inputs amount to 76.6 ± 27.8 kg N ha^{-1} year^{-1} and 2.0 ± 0.7 kg P ha^{-1} year^{-1}, that is a reduction of 56% of N deposition and 97% of P deposition.

3.4 | Uncertainty and variability in model parameters: Bootstrap approach

The resampling approach across 999 bootstraps samples propagating variation and uncertainty into our estimates of N and P concentrations of urine and faces, urine volume, faeces mass and dog residence times resulted in mean inputs of 12.2 kg N ha^{-1} year^{-1} (with 5 and 95 percentiles of 0.0 and 63.2 kg N) and 5.2 kg P ha^{-1} year^{-1} (with 5 and 95 percentiles of 0.0 and 24.1 kg P) (Figure S1).

4 | DISCUSSION

4.1 | Fertilization by dogs is substantial and non-negligible

Dogs appear to be a non-negligible, substantial and underestimated source of nutrients into peri-urban ecosystems. Dog N input was 11.5 kg N ha^{-1} year^{-1} across all sites, with a peak of 31.3 kg N ha^{-1} year^{-1} in the study site with the highest dog densities. The dog P input was 4.8 kg P ha^{-1} year^{-1} across all sites, with a peak of 13.1 kg P ha^{-1} year^{-1} in the site with most dogs. Our estimates become even more significant when compared to (i) the potential annual nutrient removal rates with mowing and hay removal (traditional management in semi-natural grasslands) that amount to 10–70 kg N and 2–20 kg P ha^{-1} year^{-1} in grasslands (Oelmann et al., 2009; Schelfhout et al., 2015) and (ii) atmospheric N deposition inputs

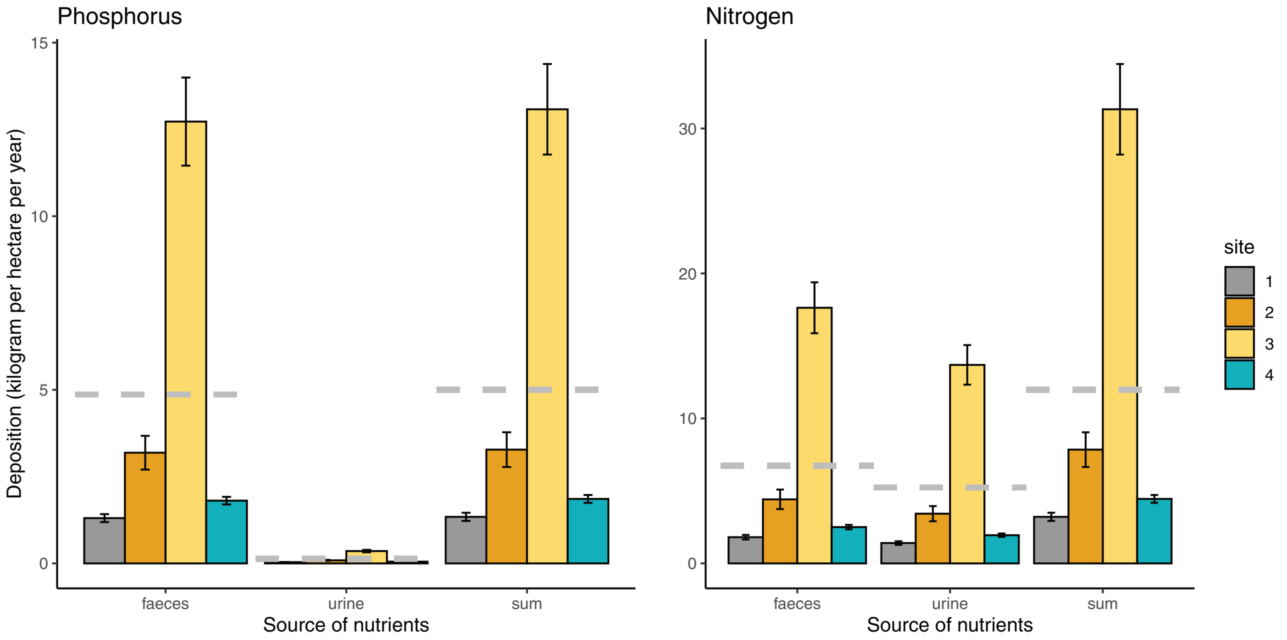

FIGURE 3 Estimated inputs (kg ha^{-1} $year^{-1}$) of phosphorus (P) and nitrogen (N) via dog fertilization as faeces and urine, and their summed contributions, across the four study sites. Error bars denote standard errors. The grey dashed lines represent the mean across the four study sites

(5–25 kg N ha^{-1} $year^{-1}$ across most of Europe; based on EMEP data in Staude et al., 2020).

Unlike atmospheric N or fertilizer N and P in grasslands under agricultural use, nutrients deposited by animals are not deposited uniformly, but in patches. Carnivores, for instance, have the tendency to deposit faeces on (aboveground) landmarks, for example near entrance gates and trail intersections (Oates et al., 2017). In the case of dogs, urine deposition is patchy, even when only 1 m away from park paths (Allen et al., 2020). Half (44%) of the N deposited by dogs is via their urine. Within urine patches deposited by grazing sheep and cattle, the N loads are in the range of 500–2000 kg N ha^{-1}. The N deposit in a dog's urine patch is expected to be even higher as dog urine (18.7 g N L^{-1}) (Table S1) is more concentrated than cow (0.7–10.2 g N L^{-1}) or sheep urine (1.4–6.1 g N L^{-1}) (Hoogendoorn et al., 2010). The N in urine has a very rapid effect on vegetation: within 2 days after excretion, it is completely transformed in plant available forms of N (ammonia and nitrate) (Lantinga et al., 1987). The N deposited in urine patches, however, is prone to losses through volatilization (NH_3) or leaching (NO_3^-) depending on vegetation, soil type, temperature and precipitation. Research on the fate of urine N of grazing dairy cows shows that the proportion of the N recovered in the herbage varies between 58% and 32% for spring and autumn applied urine, respectively (Decau et al., 2003). An important but unknown part of the N deposited in winter and autumn will not be taken up by the vegetation in the urine patches but is prone to leaching and volatilization.

Only 3% of the total P deposited by dogs is via their urine. Unlike N, P in the soil is much less mobile and will become gradually available to plants in the next growing seasons (Jarvis, 2000). The P and N deposited through faeces thus represent 97% and 56% of the total deposited P and N, respectively. This portion is less prone to leaching or volatilization losses and will become more gradually available for plants compared to urine. These nutrients will only affect the vegetation in the direct neighbourhood of the place where the faeces was deposited: for instance, cattle dung pats covering 0.05 m^2 affected grass growth in an area of about 0.25 m^2 surrounding the dung and can have a measurable effect on grass growth for up to 2 years (Lantinga et al., 1987).

4.2 | Effects on biodiversity

It is clear that the levels of fertilization by dogs estimated here can potentially exert negative effects on biodiversity and ecosystem functioning of species-rich vegetation that are often pursued in forest and nature management. Higher nutrient levels lead to increased plant growth, mostly by a limited number of nutrient-demanding species that will outcompete specialists, particularly by taking away the available light (Hautier et al., 2009), causing plant species loss (De Schrijver et al., 2011) and homogenization of plant communities (Staude et al., 2020). This well-known effect of N pollution on vulnerable ecosystems has led to the concept of *critical deposition loads*, which is defined as the limit ('effect threshold') above which habitat quality risks to be significantly damaged by the impact of N deposition (Bobbink et al., 2010; Wamelink et al., 2021). For the vegetation types of our study sites 1–3, this critical deposition load is 20 kg N ha^{-1} $year^{-1}$, whereas it ranges for study site 4 between 20 and 34 kg N ha^{-1} $year^{-1}$ depending on the vegetation type (Van Dobben et al., 2012). With a current atmospheric N deposition of 5–25 kg N ha^{-1} $year^{-1}$ across most of Europe (Staude et al., 2020), it is clear that the estimated canine N input of 11.5 kg N ha^{-1} $year^{-1}$ can have an important additional impact. Specifically, within the urine patches N deposition has a strong effect on plant biodiversity and ecosystem processes (e.g. carbon and nutrient cycling) on a microscale. On-site management such as mowing with hay removal can compensate much of the negative effects of N deposition, but mostly fails to reduce the ecosystem N levels due to the constant input through deposition and is relatively expensive (Jones et al., 2016). It is highly questionable that on-site management can also compensate the negative effects of N deposition in dog urine patches, given the much higher concentrations compared to more uniform atmospheric deposition.

Also, excess P, most often due to former agricultural fertilization, has a well-known negative effect on plant species richness (Ceulemans et al., 2014; Schelfhout et al., 2021; Wassen et al., 2021). Moreover, in contrast to N, P is one of the least mobile mineral nutrients and legacies of P fertilization can last for centuries (Schelfhout et al., 2017). This P immobility leads to difficult and slow on-site P removal management. Heavily fertilized, intensively managed agricultural grassland in Belgium yields about 14 mg dry matter ha^{-1} year^{-1} and exports 52 kg P ha^{-1} year^{-1} (Cougnon et al., 2018). In *Nardus* grasslands under restoration, however, removal rates are 2–20 kg P ha^{-1} year^{-1} under mowing with hay removal (Schelfhout et al., 2019). More drastic restoration techniques such as phytomining and topsoil removal can increase P exports, but are also more expensive and have strong impacts on other abiotic properties. Because the average P fertilization by dogs in our study almost levels the annual export rates by mowing with hay removal, it is clear that dogs can potentially have a strong impact on the vegetation and the management of these sites. Currently, these sites are under restoration management and mowing with hay removal is applied to reduce P levels in the soil to promote plant biodiversity; this process will be significantly slowed down by the import of canine P. In the forests, the current management of no intervention and low-density livestock grazing is less oriented towards P removal, but these management types presume a more or less closed P-cycle. Also, here, the effects of continuous P fertilization by dogs can eventually lead to eutrophication.

4.3 | Recommendations for management: Applications

Given the potentially high fertilization rates by dogs in peri-urban ecosystems, guidelines for management should be directed towards moderating these inputs such that critical load exceedance, biodiversity loss and delay of restoration goals be avoided. Based on our results, we propose land managers, especially in ecosystems with species adapted to nutrient-poor soils, take actions to (i) stimulate visitors to take away solid faecal waste (the most important source of P) by emphasizing the fertilization effect of their dogs in addition to other more widely known negative impacts, for example on wildlife, (ii) enforce leash use more stringently, (iii) establish more off-leash dog parks and (iv) consider more often entire dog bans in oligotrophic ecosystems. First, as faeces contained 97% of the P and 56% of the N deposited, taking away the faeces using, for instance, disposal bags and pooper-scooper stations can greatly decrease potential nutrient enrichment (see Oates et al., 2017 for a discussion of other, more expensive management options). In addition, removing dog faeces prevents the infection of grazing animals with zoonotic diseases, such as *Neospora caninum*. Dogs are the definitive hosts of this obligate intracellular parasite, but many other animal species can get infected. In wild ruminants like roe deer (*Capreolus capreolus* L.) but especially domesticated grazers like cattle and sheep, infection with *Neospora* is a main cause of abortion (Almería, 2013). Our findings also underpin that a 'stick and flick' strategy to reduce the nuisance of treading in dog faeces (as currently considered by, e.g., the Forestry Commission in Britain) is to be avoided. Second, keeping the dogs leashed (short leashes of ~2 m) concentrated the depositions in the vicinity of the trails saving the rest of the area, but this then results in very high deposition rates of 175 kg N ha^{-1} year^{-1} and 73 kg P ha^{-1} year^{-1} near the paths. This N dose even nearly corresponds to the legal threshold set by the EU Nitrate directive (91/676/EEC) for N from livestock manure in the European Union. At this fertilization level, grasses dominate the vegetation and many forbs are outcompeted. A survey on French permanent grasslands, for example, showed that once N fertilization exceeds 150 kg N ha^{-1} year^{-1}, a presence of more than 10% legumes in the biomass becomes very rare (Jeuffroy et al., 2015). The P dose of 73 kg P ha^{-1} year^{-1} largely exceeds the local legal threshold for fertilization of agricultural grassland and arable land (i.e. 30–50 kg P ha^{-1} year^{-1} depending on the P concentration of the soil) and the potential P export through the grass harvest (see above). Leashing dogs and removing their faeces reduced deposits to 77 kg N ha^{-1} year^{-1} and 2 kg P ha^{-1} year^{-1} in the vicinity of the path. The mowing frequency near the path could of course be enhanced (e.g. five to eight times per year) to export more nutrients than the rest of the area. Third, enforcement also seems to have a clear effect when we compare data from site 1 where off-leash dogs only accounted for 8% of total dog numbers (a law enforcement officer strictly cautions and, on second infringement, fines every off-leash dog owner) with sites 2–4 where the legal obligation to leash dogs is not enforced and off-leash dogs represented 29%–49% of dogs. [Correction added on 7 February 2022 after first online publication: percentages have been updated 9% and 27%–52% to 8% and 29%–49%.] Obviously, enforcing codes does not always change behaviour (Oates et al., 2017). Fourth, specifically designed nearby fenced off-leash dog parks where dogs are allowed to roam freely, together with a dog ban in sensitive oligotrophic ecosystems with plants adapted to nutrient-poor soils, could take away the pressure on areas that are important for biodiversity conservation. Finally, the hitherto often neglected fertilization effect by dogs should better be included in management plans, in media campaigns and in public education programs with regard to dogs in (semi-)natural peri-urban ecosystems.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHORS' CONTRIBUTIONS

All authors conceived the study design and co-wrote the paper. P.D.F., G.P.J.J. and P.V.G. collected and analysed data.

DATA AVAILABILITY STATEMENT

All raw data and code are available via figshare at https://doi.org/10.6084/m9.figshare.17054171.v1 (De Frenne et al., 2021).

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