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Changing Bird Migration Patterns Have Potential to Enhance Dispersal of Alien Plants From Urban Centres

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ABSTRACT

There is increasing recognition that alien species may be ‘sleepers’, becoming invasive with favourable changes in conditions, yet these changes remain difficult to predict. As populations of frugivorous birds shift with urbanisation and climate change, they could provide dispersal services for introduced fruiting plants that have previously been considered benign. This is likely to be especially problematic at higher latitudes where bird migration phenologies are altering rapidly. However, any consequences for fruit dispersal have not yet been explored. Here, we use Helsinki, Finland, to investigate whether (i) streetscapes provide birds with a fruit resource that differs from urban forest fragments and (ii) the chances for dispersal of alien species (i.e., preferential consumption of native fruits). While there were both more fruits and birds in streetscapes (replicated across multiple years), fruits were not consumed preferentially according to origin. Additionally, seed analysis from faecal samples of blackbird *Turdus merula* L., a previously migratory but increasingly resident species, suggested that alien and native plants are equally likely to be dispersed. These results indicate that birds could be dispersing alien species more frequently than previously thought and highlight the complex effects of changing climates on potentially invasive species.

1 | Introduction

Cities are hotspots for the introduction of alien flora (Pysek 1998), either accidentally or intentionally through gardening and horticulture (Seebens et al. 2017). However, whether these species spread into surrounding natural habitats depends on their dispersal agents—if there are limited opportunities for flora to disperse from urban areas, then the risk of invasion is low (von der Lippe and Kowarik 2008). While many species already known to be invasive are now well studied (Simons 2003), it is still hard to determine on a case-by-case basis if a species introduced into a particular place could become invasive in the future. This is further complicated

by the emerging realisation that populations of alien species can be present in an environment at low abundance, but not spread unless environmental conditions become more favourable (i.e., ‘sleeping populations’) (Spear et al. 2021). Therefore, while life-history traits of the plant (e.g., life span or mode of reproduction) are critical to the dispersal potential of a species (Sutherland 2004), they may nevertheless be currently limited by a lack of dispersers or other mutualisms (Richardson et al. 2000). While missing mutualisms may be provided by the introduction of other alien species (Richardson et al. 2000), changing environmental conditions are also likely to influence the presence and abundance of native species who can increasingly take on this role.

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In the case of fleshy-fruited plants, the dispersal of seeds is a key step in the spread of a species (Richardson et al. 2000). Excluding transport by humans, endozoochory and ectozoochory, that is transport of seeds via the digestive passage of vertebrates and on the bodies of animals, respectively, lead to seeds transported the longest distances (Vittoz and Engler 2007). Seed dispersal of fleshy-fruited plants by birds is an example of endozoochory. Endozoochorous frugivorous birds are abundant in urban areas and are known to move easily among habitat patches (Gelmi-Candusso and Hämäläinen 2019). Therefore, they are likely to aid the spread of alien plants into more natural areas from urban centres (Buckley et al. 2006). Generalist birds thrive in urban areas (Ducatez et al. 2018) and growing urbanisation and biotic homogenization (McKinney 2006; Schneiberg et al. 2020) encourage the interaction of these generalists with alien plants (Gray and van Heezik 2016). Not only do alien plants provide native birds with food resources in urban areas (Gray and van Heezik 2016), but the presence of alien plants has also been observed to increase the consumption of fruits from native plants (Vergara-Tabares et al. 2022). However, the scale of the contribution of birds in the spread of alien plants from urban centres into natural areas remains unclear.

In temperate regions, a majority of fruit is produced in the autumn (Thompson and Willson 1979). However, with anthropogenic climate change, there has been a marked shift in the onset and duration of autumn, with warmer temperatures in turn affecting the phenology of plants and animals (Gallinat, Primack, and Wagner 2015). In many cases, warmer autumn temperatures and the resulting extended growing season can give alien species an advantage over native plant species (Fridley 2012), especially at more northern latitudes (O'Connell and Savage 2020). To prepare for migration or winter conditions, many bird species consume fruits opportunistically (Kanerva et al. 2020; Newton 2010), even if in other seasons they are not predominantly frugivorous (Parrish 1997). However, changes have also been observed in the timing of autumn migration, with warmer temperatures and increasing availability of resources meaning more species are either delaying migration or even beginning to remain in situ during the winter (Jenni and Kéry 2003; Lehikoinen and Jaatinen 2012; Van Buskirk, Mulvihill, and Leberman 2009) (e.g., Eurasian blackbirds *Turdus merula* L.: Møller et al. 2014). Together, these changing phenologies may therefore have resulted in a novel situation where more birds can now potentially consume the fruits of alien species (Hobbs et al. 2006). As temperatures and urbanisation are predicted to keep increasing, it is crucial to understand what such changes in phenology might mean for the spread of alien species out of urban areas.

Here, we use Helsinki, Finland, as a case study to explore the interactions between changing distributions of native avian frugivores and the native and alien fleshy-fruited plants available to them. Located at 60° N, the city is experiencing large variations in local climate, with warmer winters and earlier springs due to climate change (Rantanen et al. 2022). There are currently 15 species of plants recognised as harmful invasives of national importance in Finland (<https://vieraslajit.fi/>) and 93 alien species of fleshy-fruit bearing non-native plants have been recorded in the country after 1980 (University of Helsinki 2024) and have potential to be dispersed beyond their introduction site with

changes in frugivorous bird communities (Spear et al. 2021). For example, abundant generalist frugivores are important to the maintenance of ecosystem functions (Vitorino et al. 2022) and species such as Eurasian blackbirds (*Turdus merula* L., hereafter blackbird) and Fieldfare *Turdus pilaris* L. have been increasing and expanding rapidly northwards in Finland in recent decades (Bosco et al. 2022; Lehikoinen and Virkkala 2016; Meller et al. 2016). This change has also been accompanied by a shift in migration phenology (Møller et al. 2014) with many individuals now remaining residents during the autumn and winter (i.e., partial migration). To determine the potential for alien plant species in Helsinki to be 'sleeper' populations, we therefore (i) surveyed the distribution and seasonal availability of native and alien fruit-bearing plant species in two urban habitats: private gardens and public avenues (hereafter, streetscapes) versus forest fragments (Figure 1). Then (ii) we explored if the relative abundance of potential avian dispersers (frugivorous birds) differed in these two habitats. We predicted that there would be more alien fruits in streetscapes than forest habitats, especially later in the season, but that birds' relative abundances would not vary as the species of birds consuming fruits are habitat generalists. Next, we used (iii) field observations of fruit consumption to determine whether there are any changing seasonal preferences for native or alien fruits in streetscapes and (iv) collected direct evidence for differences in potential seed dispersal by examining faecal samples from blackbirds, the most commonly observed frugivore in our study. If changing conditions are increasing the likelihood of alien plants being spread from urban areas, we predicted that the majority of fruit consumed later in the autumn would be of alien origin.

2 | Methods

2.1 | Study Area

We focused on two different habitats within the Helsinki urban area: streetscapes and urban forest fragments. Streetscapes are comprised of private gardens and municipal street plantings that contain a mix of native and alien species (Figure 1) chosen by residents or municipal departments, respectively. Forest fragments (Figure 1) are maintained for recreational use, for example running, walking or cycling, and to preserve biodiversity values and resemble similar forest types outside the city (Korhonen et al. 2020). Helsinki has a relatively large and diffuse interface between urban and more natural forested areas as urban forest fragments occur in a semi-connected matrix from downtown to the edge of the metropolitan area (Hautamäki 2019). Urban forest fragments therefore may provide a potential stepping stone habitat for introduced plants to establish and move into more natural areas (e.g., Francis and Chadwick 2020) although this has not been studied for fruiting species in Finland (but see Jauni, Helenius, and Hyvönen 2012; Lampinen, Ruokolainen, and Huhta 2015 for other plants).

2.2 | Field Observations

To survey fruit availability and bird feeding behaviour, we used 15 transects (100 m long by 10 m wide) within streetscape and forest fragment habitats (i.e., $n = 30$ transects in total; Figure S1;

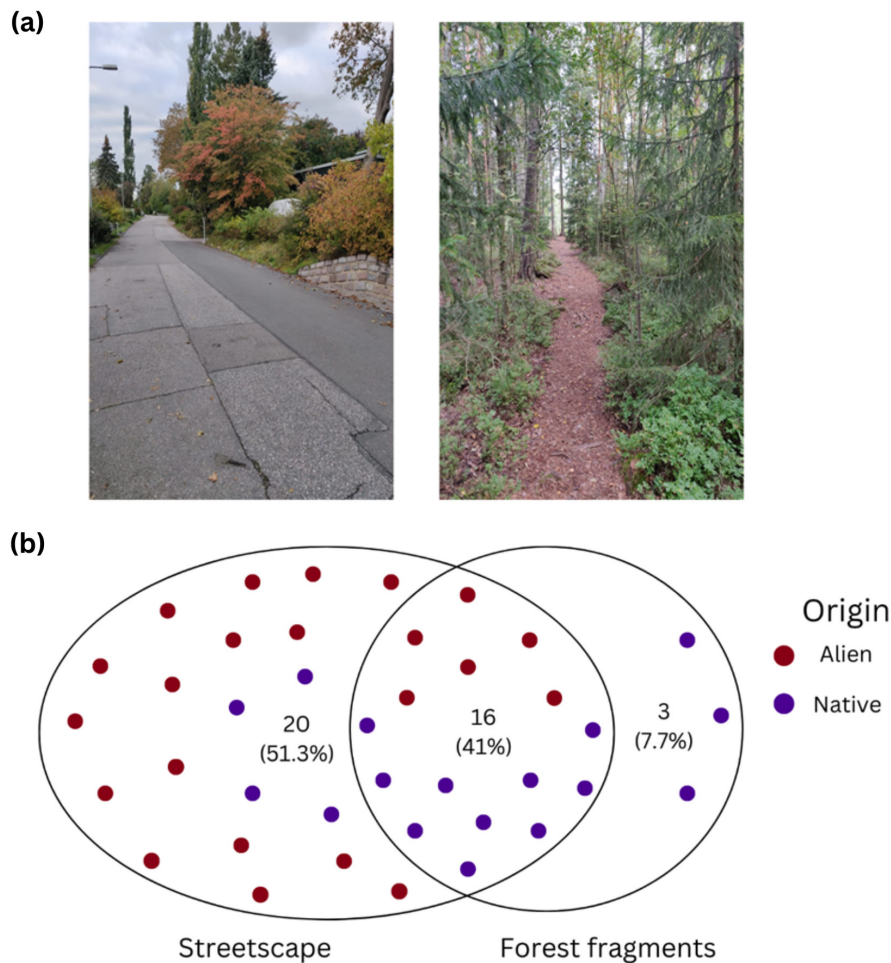


FIGURE 1 | (a) Typical habitats along transects in streetscapes and forest fragments and (b) Venn diagram illustrating the number of fruiting plant species found in the two habitats (sampling area $n=1500\text{ m}^2$ of transects in each habitat) according to origin (red dots=alien plants, blue dots= native species; list of species in Table S1).

Table S2). The location of each transect was determined using an online random number generator to select an area from a $1\text{ km} \times 1\text{ km}$ numbered map grid; the start of the transect was then assigned by finding a point within the selected map area that provided sufficient space for the transect length and was not near busy roads. The closest distance between two transect starting points was approximately 250m. Transects were selected such that they were representative of the plant communities in the area and had more than three plant species. The plant communities surrounding transects were more similar between the different transects in forest fragments, while in streetscapes they tended to vary as a result of the plantings people chose to make around their homes. Each transect was sampled once in the first 10 days of each month from August to November in 2019, 2020, and 2021. Due to travel restrictions during the COVID pandemic, however, observations in 2020 were made only during October and November. Furthermore, as 2020 was a poor fruiting year over all and specifically for rowan *Sorbus aucuparia* L. and bilberry *Vaccinium myrtillus* L. (Gallego Zamorano, Hokkanen, and Lehikoinen 2018), resulting in most forest fragment transects not having any fruits by October. Hence, data was only collected from transects in streetscapes in 2020 as forest transects did not have any fruit in the later autumn months when sampling was possible. To account

for variation in bird activity within a month, 10 transects (5 transects per habitat) were sampled again during the last 10 days of each month. As there was a wide variation in the daylight hours during the autumn, morning observations were made from 30 min after sunrise to 3.5 h after sunrise. Evening observations were carried out from 16.00 to 18.00 in August and September and from two and a half hours before sunset to half an hour before sunset in October and November. Each transect was equally sampled in the morning and evening.

During each sampling visit, the abundance of potential seed-dispersing bird species and their feeding activity was observed by walking slowly along the transect for 30 min in total (all observations by P. Deshpande, using binoculars). When a bird was seen in a plant on the transect, we recorded the species of plant that the bird was in and, if feeding, the number of fruits the bird ate. If there were multiple birds eating fruits on a plant, individuals were observed in turn until its feeding bout ended (moving away and not to another bunch of fruits on the same plant). Then, the next bird in the plant was observed until its feeding bout ended and so on. As the number of observations of actively feeding birds was lower than expected in the first years of the study, in 2021 we included observations of birds perched in any location along the transect to represent the relative abundance

of fruit eating birds around the transects. We did not count birds that were only heard, as it was difficult to determine if an individual was counted twice based solely on the calls. Birds can be easier to detect in streetscapes as they have more open areas than forests. To measure the potential detectability differences between the two habitat types, we then sampled 4 random transects from each habitat again in October 2022. Birds were observed within 5 m, 10 m, 25 m and > 25 m bands but we found little difference in detectability function according to habitat (using the 'Distance' package: Miller et al. 2019; average probability of detection: Streetscape = 70.1%; Forest fragments: 66.3%; $z = 0.255$, $p = 0.798$).

After 30 min of observing birds along the transect, the number of fruits present on each plant species was estimated. On each individual plant or hedge, the number of fruits was counted from five "bunches" or along five branches, depending on how the fruits were arranged. The average was then multiplied by the number of bunches/branches visible on the plant. As it was not always possible to see the whole plant, we estimated the percentage that was visible and took this into account when calculating the number of fruits available. For bilberry, which often grows continuously as groundcover over large areas, we estimated the fruit number from 1 m of the ground covered by the plants and then multiplied this by the length of transect where the species occurred. Fruit availability was recorded until fruits were no longer seen on a plant or until the end of the sampling period in November. Bird observations were only made while there were still fruits on the transect as we were primarily interested in understanding which fruits birds ate. Additionally, in the first year of sampling, we did not observe any frugivorous birds on transects where there were no fruits.

Plants were identified using the PlantNet app (Goëau et al. 2013) and when needed, the identification was verified using local floras, checklists, online resources and expert consultation (Kurtto et al. 2023; Väre et al. 2021). Plant origin was classified as native or alien based on a published checklist (Kurtto et al. 2023) and metadata in the laji.fi portal of the Finnish Biodiversity Information Facility (FinBIF; Kurtto et al. 2023). All cultivars and domesticated species of plant breeding origin were considered alien unless specifically stated as native in FinBIF. In those groups where species- or cultivar-level identification was not possible (some *Crataegus* spp., *Malus* spp., *Rosa* spp.), a generic classification was used (see Table S1). Of the alien species observed on the transects, only *Rosa rugosa* Thunb. is recognised at the national level as a harmful invasive (<https://vieraslajit.fi/>).

2.3 | Faecal Sample Collection and Seed Identification

Faecal samples were collected opportunistically from blackbirds between August to October during 2018 to 2020. Apart from being the most common frugivorous species on the transects, blackbirds are relatively large and can swallow most fruits whole, hence making them more likely to transport seeds as compared to smaller bird species. Licensed bird ringers (Authors E. Klun and R. Thorogood) caught and handled all birds as part of a different project, and the faecal samples were collected either while

the birds were in clean bird bags waiting to be ringed or when the birds defecated while being measured. The samples were transferred immediately to individually labelled plastic bags and stored in a freezer (-20°C). Blackbirds were caught at three sites in urban areas across greater Helsinki that represented similar habitats to the transects (i.e., streetscapes and forest fragment matrix), although they were not in identical locations. Samples were only collected from individually identifiable (i.e., ringed) birds to avoid pseudoreplication.

Seeds were isolated from the sample by washing in a tea sieve under cold water and over a funnel lined with filter paper to ensure no small seeds were lost. The cleaned seeds were then dried on tissue paper and stored in paper seed bags or small plastic bags in a freezer until identification. Identification was performed (by authors N. Johansson and P. Deshpande) using reference seeds collected from the field or botanical collections of the Finnish Museum of Natural History, or using identification guides (Cappers 2014) and photographs (Table S3). In total, 182 faecal samples were collected. Of these, 70 samples did not contain any seeds and from seven samples, we were unable to identify 12 seeds due to species ambiguity or damage.

2.4 | Statistical Methods

All statistical analyses were carried out in R version 4.2.1 (R Core Team 2022). All the data and code are publicly available on an online repository (Deshpande 2024).

2.4.1 | Differences in Fruit Availability Between Habitats, Across the Season

To identify if alien plants from streetscapes might be moving to forest fragments, we first used a Permutational multivariate analysis of variance (PERMANOVA; vegan package: Oksanen et al. 2019; visualised as a Venn diagram using package 'ggvenn': Yan 2022) to test whether there were differences in the occurrence of plant species of alien and native origin in the two habitats. We only used the data collected during the last study year (2021) as new plants were noted growing on the transects as the study progressed. Next, we tested whether the availability of fruits varied seasonally and differently among the two habitats (using data from all 3 years of the study) to determine whether these varied in overall abundance of fruit food resources. Initial data visualisation suggested that the availability of fruits overall increased until mid-autumn and subsequently decreased. To account for this non-linear seasonal pattern, we used Generalized Additive Mixed Models (GAMMs) with a Poisson error distribution (using the 'mgcv' package: Wood 2011). As habitat (street-scape or forest fragment) and plant origin (native or alien) were correlated ($\chi^2 = 258,960$, $df = 219,064$, $p < 0.001$), we constructed separate GAMMs for each habitat to investigate the different availabilities of native and alien fruits. In all models, the independent variable day-of-year was included with a smoothing function, with separate curves allowed for the origin of plants. Transect number was added to all models as a random effect to control for repeated observations and year (3 levels, according to Oberpriller, de Souza Leite, and Pichler 2022) was added as a random effect to control for the natural variation in the amount

of fruit produced across years. We tested for the additive and interactive effect of the variables and selected the most parsimonious model using AIC values, where the model with the lowest AIC value ($\Delta\text{AICc} > 2$) was taken as the minimally adequate model (Burnham and Anderson 2004). The goodness of fit of the model was checked using the 'gam.check' function of the 'mgcv' package. There were two native plant species on the transects with orders of magnitude more fruit (rowan and bilberry) so we also ran analyses without these two species included.

2.4.2 | Differences in Bird Relative Abundance Between Habitats, Across the Season

To investigate changes in the relative abundance of potential seed dispersing birds in the different habitats across the season, we only analysed data from 2021 as this had the largest sample size (see Methods (b) Field observations). We first modelled the number of birds overall using a GAMM with Poisson error distribution, with habitat type and week in the year included as explanatory independent variables (we used week rather than day of the year as there were fewer observations of birds across the season than there were for the number of fruits). Week of year was included with a smoothing function, with separate curves allowed for the origin of plants and transect number included as a random effect to account for repeated sampling. Both the additive and interactive effects of the two independent variables were tested and the model with the lowest AIC value was selected as the most parsimonious model (Burnham and Anderson 2004). Next, we investigated whether these patterns varied according to migration strategy by modelling the summed abundance of birds on a given transect within each category (migrant, partial migrant and resident as classified by Piha, Valkama, and Lehikoinen (2018); Piha and Lehikoinen (2015). Other explanatory variables and the random effect structure were the same as for models of overall bird abundance, but these data were better modelled using a negative binomial error structure (the suitability of model fit was assessed with residual diagnostics carried out using the 'DHARMA' package: Hartig 2022).

2.4.3 | Preferences in Type of Fruit Eaten Across the Season

Across all 3 years of sampling, there were only eight instances when birds were observed eating fruits in forest fragments and none of these fruits were of alien origin. Hence, we only conducted this analysis using data from streetscapes, as the question of interest was whether it was possible for alien species to be transported out of the area of introduction. Additionally, due to COVID restrictions, we could only collect data for 2 months in 2020; hence, this data was excluded from the analysis. We summed the number of fruits eaten for every species of plant on a transect during a given survey (hereafter, fruits eaten) and the number of ripe fruits present per species of plant on a transect on a given day. These were then used as a bound proportional response variable (using the cbind function) in GLMMs and GAMMs with binomial error structure. Origin (native or alien) and week were added as independent variables and the transect replicate nested within the transect number was added as a random effect to account for multiple rows of observations from

each sampling visit. Additionally, to account for variation in the number of fruits produced by different species of plants, plant species were also added as a random effect. As in the previous models, the best model between the additive and interactive effects of the covariates was selected using the lowest AIC values.

2.4.4 | Potential Seed Dispersal by Blackbirds

First, we tested whether blackbirds dispersed higher numbers of alien versus native seeds through the season using GLMMs with Poisson error distribution (we did not have sufficient observations for GAMMs) and the number of seeds per plant species within each sample as the response variable. Origin of seeds (native or alien), year and week were included as explanatory variables. We included random effects for seed species to account for differences in size and other characteristics of the seeds and the bird's ring ID number as some samples contained seeds from multiple species. Only samples containing identifiable seeds were included in the analysis. Next, we investigated whether the proportion of native and alien seeds transported changed as the season progressed using a GLM. The number of native seeds was modelled relative to the number of alien seeds within the sample (using a bound response variable and binomial error distribution), with year and week included as explanatory variables. Each individual contributed only one row of data, so there was no random effect structure.

3 | Results

Across the study area, we recorded 39 plant species or identifiable species groups bearing fruit, of which 56% ($n=22$) were of alien origin (Electronic Table S1) and 31 species of birds (Table S4). Of these, 17 bird species were observed in 28 of the 39 species of plants and 12 of these 17 bird species were observed consuming 679 fruits in total from 12 of the 28 species of plants (Table S1). This resulted in a total of 154 events where birds were observed eating fruits across 2 years.

3.1 | Differences in Availability of Fruits and Relative Abundance of Potential Dispersers Between Habitats and Across the Season

As expected, we found that while there was a slight but statistically significant overlap in species across habitats (PERMANOVA: $F_{1,29} = 16.924$, $R^2 = 0.377$, $p = 0.001$), there were more fruit-bearing plant species in streetscapes than in forest fragments (habitat explained 37% of the variation in the proportion of native and alien plants; Figure 1; Table S5). The majority of alien species were detected only in streetscapes ($n=16$) and only four native species were recorded exclusively in urban habitats (Table S1). Sixteen species were shared between the two habitats, of which six were of alien origin. Finally, only three species were seen exclusively in forest fragments and all of them were of native origin (Figure 1b).

Overall, there was more fruit available throughout the season in streetscapes than forest fragments (Estimate = 1.664, SE = 0.527, $z = 3.158$, $p = 0.002$, Table S6; Figure 2a) but ripe

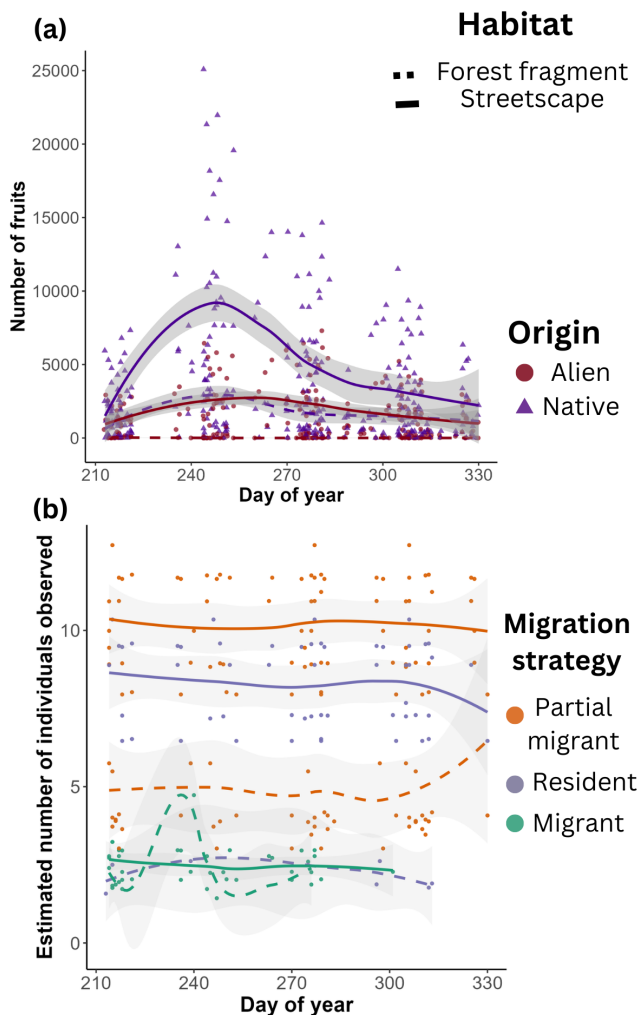


FIGURE 2 | (a) Seasonal abundance of fruits: Model predictions ($\pm 95\%$ confidence intervals, grey bands) from two separate Generalised Additive Mixed Effects Models (GAMM) estimating the seasonal change in number of fruits available of alien (red circles) or native (blue triangles) origin in streetscapes (solid regression line) and forest fragments (dashed regression line) with all the species. The points indicate the number of fruits estimated by the model for every transect ($n = 30$) every day from the end of August to the end of November (i.e., autumn at the study site) for 3 years (except for 2020 which only has data from October and November from streetscapes). Confidence intervals for alien plants in streetscapes were narrower than for native plants so are less visible when plotted, and there were few fruits of alien origin available in forest fragments (i.e., predicted line approximates zero). (b) Seasonal relative abundance of birds by migration strategy: Model predictions ($\pm 95\%$ confidence intervals, grey bands) from GLMM estimating the seasonal change in number of birds by migration strategy: Resident (purple), partial migrant (orange) and migrant (green) in streetscapes (solid regression line) and forest fragments (dashed regression line). The points indicate the number of birds estimated by the model for every transect ($n = 30$) every day from the end of August to the end of November (i.e., autumn at the study site) for 2021.

fruits from native plants were more abundant than fruits from alien plant species in both habitats (streetscapes: estimate = 0.885, SE = 0.002, $z = 407.853$, $p < 0.001$; forest fragments: estimate = 12.499, SE = 0.474, $z = 26.378$, $p < 0.001$;

Table S7a,b). There was also greater seasonal variation in the availability of native than alien fruits, with native fruits most abundant earlier in the season (Figure 2a); (Table S7a,b). These results were influenced strongly, however, by the two most common native plant species in the dataset (rowan and bilberries, 48.1% of plants across both habitats), which both bear numerous small fruits. When the analysis was repeated without these two species, alien fruits became more abundant than native fruits but only in streetscapes (streetscapes: Estimate = -1.543, SE = 0.005, $z = -293.61$, $p < 0.001$; forest fragments: Estimate = 3.291, SE = 0.217, $z = 15.177$, $p < 0.001$; Table S8a,b).

Similar to fruit availability, we also found that there were more birds in streetscapes compared to forest fragments ($n = 157$, Estimate = 1.561, SE = 0.226, $z = 6.921$, $p < 0.001$, Table S9). Unlike fruit availability, however, the relative abundance of birds increased through the season and this varied according to habitat. Forest habitats showed a slight increase in bird relative abundance as the season progressed due to partial migrants, but this was still lower than streetscapes. The abundance of birds fluctuated in streetscapes and started decreasing towards the end of the season (Table S10). When the relative abundance of birds was summarised by migration strategy, we saw that there were more partial migrants observed than residents (Figure 2b; Table S11).

3.2 | Preferences in Type of Fruit Eaten Across the Season

In streetscapes, birds did not show a preference for native or alien fruits (model accounting for fruit availability; Estimate = -1.468, SE = 1.561, $z = -0.94$, $p = 0.347$; Table S12; Figure S2). A non-linear pattern was seen in the proportion of native fruit consumed through the season ($\chi^2 = 112.195$, $p < 0.001$; Figure 3a; Figure with data points: Figure S3), but there was no statistically significant difference detected between the mean proportion of native and alien fruits consumed across the season (Table S13). Blackbirds *Turdus merula* L., blue tits *Cyanistes caeruleus* L., greenfinches *Chloris chloris* L. and bullfinches *Pyrrhulla pyrrhulla* L. were the species most frequently seen eating fruits on the transects (Figure S2). All of these species are also listed as partial migrants in Finland (Saurola, Valkama, and Velmala 2013), possibly indicating that a change in their migration phenologies could influence changes in seed dispersal.

3.3 | Potential Seed Dispersal by Blackbirds

From 91 faecal samples with intact seeds, we extracted 138 alien and 413 native seeds (Table S3). We found that there was no difference between the absolute number of alien or native seeds carried by blackbirds in our sample (Estimate = -0.009, SE = 0.303, $z = -0.026$, $p = 0.979$; Table S14). Based on our results of seasonal variation in fruit availability (i.e., Figure 2a), we expected that proportionately more alien seeds would be transported later in the season. However, we found no evidence for seasonal variation in the proportion of native and alien seeds transported (Table S15).

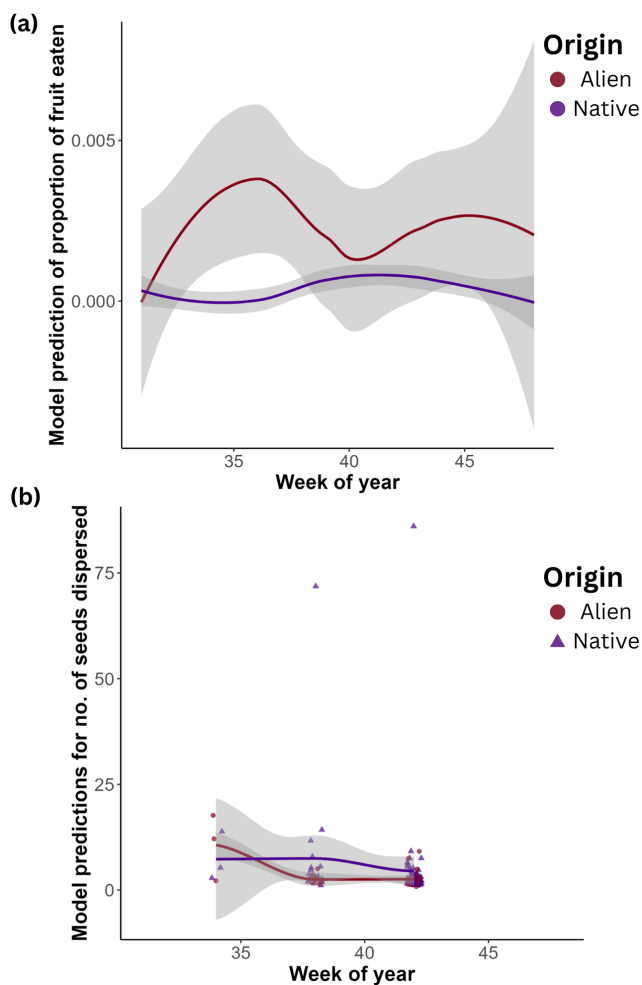


FIGURE 3 | (a) Proportion of fruit eaten with respect to fruits available: Predictions from GAMM estimating the proportion of fruits eaten [alien (red) or native (blue) origin] in streetscapes to the number of fruits available on the transects of each origin. The trendlines indicate the estimated proportion of fruit eaten of the fruit available by the model for every transect ($n = 15$) in sampling days from the end of August to the end of November (i.e., beginning of winter at the study site) for 2 years. Here we do not show data points for ease of viewing trendlines, for plot with data points see Figure S3 (b) Number of seeds found in faecal samples of blackbirds: Predictions from GLMM estimating the number of seeds of native and alien origin found in blackbird faeces ($n = 117$) over 2 years.

4 | Discussion

Changes in the phenology of plants (O'Connell and Savage 2020) and animals (Gallinat, Primack, and Wagner 2015) and the introduction of alien species by humans create an opportunity for novel interactions (Walther 2003). Such novel interactions can aid the dispersal of alien plant species (Cruz et al. 2013). However, this spread of alien species can be hard to detect or predict until after they have established (Simons 2003; Spear et al. 2021). Here we investigated seasonal patterns in the relative abundance of birds and abundance of fruits of native and alien origin across streetscapes and forest fragments in Helsinki, an urban area experiencing rapid changes in climate and biodiversity (Leppänen et al. 2024). We found that compared to urban forest fragments, there was more fruit available overall

in streetscapes and, perhaps not surprisingly, frugivorous birds were also more abundant. After taking the super-abundant but mast-fruiting rowan and bilberry into account (the most commonly available fruiting native species), more of the fruit available in streetscapes was of alien origin than in forest fragments and alien fruit availability peaked later in the season than fruits from native plant species. However, there was little evidence from either feeding observations or faecal samples that frugivorous birds preferred to consume either native or alien fruits. Together, these results suggest that dispersal of alien fruiting plants may be possible and that continued changes in the migration phenology of birds in the area are likely to lead to an increased risk of invasion.

'Sleepor populations' are defined as alien species that occur in low abundance (at or beyond their site of introduction) until a change in an environmental factor enables a rapid increase in population size and a shift in ecological impact towards invasiveness (Spear et al. 2021). It is not always clear, however, when an occasional detection of an alien species in the wild represents dormancy or is at the beginning of an outbreak and a major question concerns determining how long a putative sleeper population will persist before it goes locally extinct or erupts (Spear et al. 2021). While we could not track individual birds moving seeds directly between habitats, we nevertheless located six alien plant species in both streetscapes and forest fragments. Furthermore, birds were observed to consume fruits of all these species and seeds of all but one species were identified in the blackbirds' faecal samples. All of these species are recognised as aliens but not as harmful invasives in Finland and have local management strategies, but they could have potential to become invasive with increasing availability of dispersers (Supporting Information: Section A). For example, red elderberry *Sambucus racemosa* is found in forest edges and over the 3 years of our study, we observed that red elderberry along forest transects increased each year. One of the other species we detected, Dwarf serviceberry *Amelanchier spicata*, is a species of concern as it can suppress the growth of native species (Lanta, Hyvönen, and Norrdahl 2013) and is recommended to be removed from streetscapes, gardens and replaced with, for example, black chokeberry *Aronia x prunifolia* for its similar autumn colours and berry crop (Finnish Advisory Board for Invasive Alien Species 2023). However, as we also observed birds consuming fruits and carrying seeds of *Aronia x Prunifolia* and detected it within our forest fragments, the status of this alien species in Finland should be updated. By observing bird-plant interactions, our results show that these potentially problematic species are being dispersed from their sites of introduction in streetscapes into more natural areas and are likely to be 'sleeper populations' while still in low abundance. Continued monitoring will be necessary, however, to determine how these populations develop.

For alien plant species to spread beyond urban areas, they require active dispersers that move among a habitat matrix and deposit the seeds into favourable areas (Alden 2004). All of the bird species feeding on fruits in our study area are likely to do so opportunistically to improve their body condition for autumn migration or to prepare for a harsh winter climate if they remain resident in Finland (e.g., similar to Parrish 1997; Carter et al. 2021) and at a time when they show little territoriality (Lundberg 1985)—this can result in dispersal over larger

distances. Earlier studies have highlighted how different types of habitats and birds' movements across them aid the movement of nutrients (Fujita and Koike 2009; Tremblay and St. Clair 2011). Additionally, the abundances of common frugivore species like blackbirds have increased approximately four times since the 1980s in Finland (Lehikoinen and Väisänen 2022). We expected to find no differences in the relative abundance of birds between streetscapes and forested areas as both habitats were part of an urban matrix and the majority of bird species observed eating fruits are commonly observed in urban areas. However, we found that birds were more abundant in streetscapes as compared to forest fragments, even after we accounted for possible differences in detectability. This could potentially be explained by the higher number of fruits available in streetscapes; the total pulp mass of fruits is important to birds for resource tracking rather than the nutrient content of individual fruits or species (Blendinger et al. 2015) and hence birds might be aggregating in streetscapes to make use of the abundant food resource. For omnivorous bird species, switching from an insect-dominated diet in the summer to a more frugivorous diet in the autumn is important to maintain body condition (Campo-Celada et al. 2022) and prepare for migration or harsh winter conditions. However, in areas where natural fruit availability is reduced (e.g., from habitat degradation or phenological mismatch), fruit-bearing plants in urban areas are expected to help offset the loss of fruit in more natural habitats (González-Castro et al. 2022). Therefore, the presence of alien fruiting species in streetscapes coupled with the greater abundance of birds is a cause for concern, as any increase in dependence on urban areas could aid the spread of alien species faster than in previous decades.

On the other hand, an abundance of fruit does not necessarily mean that a particular alien plant species will be dispersed, especially if native birds prefer to consume the fruits of species that they have adapted to. For example, in New Jersey (USA), birds increasingly switched from consuming native fruits to those from alien species as their availability increased into early winter (White and Stiles 1992), while at a migratory stop-over site in Massachusetts, birds primarily consumed native fruits despite alien species providing a more abundant resource (Gallinat, Primack, and Lloyd-Evans 2020). Here, we also expected native fruits to be consumed preferentially to alien fruits, but for consumption of alien fruits to increase later in the season as the peak fruiting of native species declined. However, we found that birds largely consumed fruits according to availability and not according to plant origin (i.e., there was no evidence for a preference when comparing alien and native plant species). This was, however, possibly complicated by the large number of native rowan trees planted extensively along roads and parks in Helsinki—the maximum number of fruits eaten and seeds identified from faecal samples were from rowanberries and, unlike earlier research in the countryside (Suhonen et al. 2017), we found that more rowan fruits were consumed in streetscapes than in forest fragments. Rowan trees typically have a two-year masting cycle (Gallego Zamorano, Hokkanen, and Lehikoinen 2018) and in our study period, 2020 was a year with a low rowanberry crop. However, due to the large number of trees planted in the city and those naturally growing in the forest fragments, the rowanberry fruit crop was still larger than that of any single alien species. This may have reduced the

dependence of birds on alien plants for food (and hence slow their dispersal out of the city), as there were also large amounts of fruit from alien species left uneaten. Nevertheless, fruits that remain uneaten into winter can also aid dispersal (Drummond, 2005) and in Helsinki overwintering birds are often observed to eat frozen fruit, including from many of the alien species we observed being eaten in the autumn (Personal observations PD, EK, RT and AL). Earlier research has shown that the availability of food plays a large role in influencing the number of birds that are migrating (Nilsson et al. 2006) and partial migrant species were the most abundant group of frugivorous birds in our dataset. As the autumns prolong due to climate change and the proportion of birds remaining resident through the winter increases (Meller et al. 2016), it is therefore likely that alien species may be dispersed more quickly than in the past.

It is important to keep in mind that alien plants may not always have negative consequences. For example, many studies have shown that the presence of alien fruits can facilitate the spread of native plant species (e.g., Chalker-Scott 2015; Gleditsch and Carlo 2011; Gray and van Heezik 2016). It is thought that this is because birds are attracted at first by the alien fruits and then consume those from native species nearby. We investigated in a similar fashion whether the proportion of native to alien seeds dispersed changed over the autumn, but did not find any differences in the proportion of seeds transported. Additionally, alien plants without fleshy fruit or alien species that are naturalised in the region can provide animals with an important food resource in cities experiencing biotic homogenisation (Deshpande et al. 2023; Hettinger 2001). However, with climate change, autumn and winter bird communities are undergoing rapid changes, with warm-dwelling species like blackbirds increasing across north America and Europe (Lehikoinen et al. 2021). This could further aid the dispersal of alien species that are planted across northern regions of the world and have consequences for the local plant communities and ecosystems.

5 | Conclusion

Through our case study in Helsinki, we find that in streetscapes, a majority of the plant species are of alien origin and potential frugivores are more abundant in streetscapes than forest fragments. Despite there being a large diversity of alien plants in streetscapes, the number of native fruits remained higher than alien fruits throughout the sampling period. However, this pattern was not reflected in the fruits eaten by birds, as we did not find any difference in the proportion of native and alien fruits eaten. Similarly, we do not find that alien seeds are more likely dispersed than native seeds. Our results indicate that urban birds might be opportunistically taking advantage of the vast food resource present in streetscapes and planting native plants with large fruit crops can help prevent the spread of alien species that are already seen in more natural habitats. The six species of alien plants that we found in forest fragments need to be monitored carefully, as they might be 'sleeping species' that could become invasive with changes in environmental conditions as the effects of climate change intensify in the coming years. As alien plants are introduced world over and seed disperser communities continue to change in response to global warming, our case study suggests that an abundance of native fruits can potentially aid in curbing the spread of possible

invasive plant species via frugivores. Finally, conducting more such local case studies can aid in designing policy on a case-by-case basis where alien plants that are unlikely to disperse can add to the food resource in cities and plants that are likely to because invasive are curbed before they are well established.

Author Contributions

Purabi Deshpande: conceptualization, data curation, formal analysis, investigation, methodology, writing – original draft. **Niko Johansson:** data curation, methodology, resources, writing – review and editing. **Edward Klun:** data curation, methodology, resources, writing – review and editing. **Aleksi Lehikoinen:** formal analysis, funding acquisition, investigation, supervision, writing – review and editing. **Rose Thorogood:** conceptualization, formal analysis, supervision, visualization, writing – review and editing.

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Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data and code that support the findings of this study are openly available in Zenodo at <https://doi.org/10.5281/zenodo.10089554>, versions 1 and 2.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.