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Passive environmental and group-level processes drive gut microbiome composition in a wild corvid

Eleonore Lebeuf-Taylor^{1,2*}, Andrea Meltzer^{3,4}, Saverio Lubrano^{3,4}, Karl Cottenie^{1†} and Michael Griesser^{4,5†}

Abstract

Background The gut microbiome is known from laboratory studies to be essential to host function and sociality, yet comparatively little is known about this association in wild animals. In wild birds, the gut microbiome seems to be broadly driven by environmental factors, and there is mixed evidence for a link with sociality. Here, we describe the gut microbiome composition of the Siberian jay (*Perisoreus infaustus*), a highly social group-living and food-caching corvid of the Eurasian boreal forest.

Results We present evidence of potential environment-related variation in the gut microbiome of wild Siberian jays. Environmental acquisition of microbes may be an important process shaping their gut microbiome composition based on similarities to the local environmental microbial community, for which we propose an environment–oral–gut route as a potential underlying mechanism. We also identify an unexpected group-level convergence, wherein social horizontal transmission of gut microbes may be an incidental consequence of reciprocal cache pilfering among group members.

Conclusions While the ecological significance of gut microbiome variation in Siberian jays is still unclear, our results paint a picture of passive microbiome assembly resulting from a combination of environmental acquisition and social transmission in a wild bird species.

Keywords Gut microbiome, Avian microbiome, Siberian jays, Horizontal transmission, Group-living, Sociality

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Background

Animals are living, breathing hosts for communities of microbes that inhabit micro-environments on and in their bodies. These communities are known as host-associated microbiomes [1]. The gut microbiome, found in the gastrointestinal tract, is of particular interest as it is essential for the development and function of host physiology [2], immunity [3], and behaviour [4]. The link between gut microbiome and host is bidirectional: the microbiome can directly interact with host cells and act along the gut-brain axis—the connection between the animal's brain and its gastrointestinal tract [5, 6]—while



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also being affected by physiological changes in the host [7].

The vast majority of gut microbiome studies are laboratory-based and, while they have uncovered several indisputable links between host and microbes, their relevance to ecologically realistic systems remains under debate [8]. Far from identifying mechanistic links between host and microbes, research into wild animal microbiomes is still in its early stages and mainly focuses on identifying the factors that give rise to intra- and interspecific variation. Host phylogeny [9] and diet [10], as well as environmental [11] and temporal factors [12], have emerged as broad drivers of microbiome composition in wild animals. Despite considerable variation in both microbiome composition and the relative contributions of these main factors, evidence for phylosymbiosis—the coevolution of host and microbiomes [13]—has led to the development of the holobiont hypothesis, whereby host and associated symbionts are considered a single unit of selection [14]. Whether this concept, which assumes a tight and conserved association between host and microbiome, is generalizable across the animal kingdom remains to be seen.

In addition to the potential physiological adaptiveness of the microbiome—such as its role in metabolizing otherwise indigestible molecules [15]—host-microbiome coevolution may also be linked to group living [16]. Group living in animals is an adaptive strategy that is generally thought to arise through the combined pressures of predation and foraging efficiency [17]. Group living may have additional adaptive value by enabling the exchange and maintenance of beneficial symbionts among conspecifics [18]. Indeed, social exchange of gut microbes has been observed in some group-living mammals, including yellow baboons (*Papio cynocephalus*) [19], red-fronted lemurs (*Eulemur ruffronis*) [20], and wild wood mice (*Apodemus sylvaticus*) [21, 22]. The consequences of microbial exchange within social groups, however, remain unclear and relatively little is known about the link between group living and the gut microbiome in non-mammalian species.

The avian gut microbiome is generally understudied compared to that of mammals. Broadly, the avian gut microbiome is characterized by high interindividual variation [23], with temporal and environmental factors [11, 24, 25], host phylogeny, and diet [26, 27] emerging as major drivers of intra- and interspecific variation. Unlike in mammals, evidence for vertical transmission of the gut microbiome in birds is relatively limited [28], although birds' eggs have been shown to contain a microbial community [29]. Physical contact and parental provisioning may contribute to vertical transmission in birds: junco (*Junco hyemalis*) nestlings share a similar uropygial (preen gland) microbiome with their mother [30], and the cloacal microbiomes of barn swallow (*Hirundo*

rustica) nestlings are more similar to their mother's than their father's, who provisions less [31].

Group living is widespread in birds [32] and may, like in mammals, result in interindividual microbial transmission. There is some evidence for this process: physical contact and allopreening are thought to result in the social convergence of external microbiomes, for instance in the skin microbiomes in zebra finch (*Taeniopygia guttata*) family groups [33], and uropygial gland and feather microbiomes in breeding groups of smooth-billed anis (*Crotophaga ani*) [34]. This effect, however, is not generalized: a study in common waxbills (*Estrilda astrild*) found no evidence of an effect of sociality on feather microbiomes [35]. Likewise, there is mixed evidence for a link between sociality and birds' internal microbiomes. Social contact is thought to affect gut microbiome diversity in a sex-dependent manner in barn swallows (*Hirundo rustica erythrogaster*) [36], and barn swallow pairs have more similar cloacal microbiomes [37]. However, no social effect was found in common waxbills [35] nor in bonded pairs of North American tree swallow (*Tachycineta bicolor*) [38]. While there is evidence of within-nest similarity among nestlings in barn swallows, this has been attributed to a shared environment [37]. Similarly, gut microbiome convergence among different bird species in a common area is thought to be the result of a shared environmental microbial species pool [39].

Here, we investigate the intraspecific drivers of microbiome variation among individuals of a wild group-living corvid, the Siberian jay (*Perisoreus infaustus*) [40]. Siberian jays are sedentary residents of the boreal forest in northern Eurasia who live in territorial groups consisting of two to five individuals centred around a breeding pair [41]. Non-breeders can be either retained offspring or unrelated immigrants; breeders are dominant over same-sex non-breeders [41]. Siberian jays survive the long boreal winters—which last from October to May—by caching food in lichens, under bark, and in tree crevices. Their diet is opportunistic and varies over the course of the year, from cached insects, berries, and carrion over winter, insects and carrion during the snow-free late spring and early summer, and primarily fresh berries in late summer and fall [42, 43].

Our study population has been systematically monitored since 1989, reaching a total of over 70 territorial groups today. Territories are distributed in two areas, protected (old-growth) and managed (logged) forests, the latter of which is characterized by lower-quality habitat and poorer fitness outcomes [44] (Fig. 1). Mortality in Siberian jays is predominantly due to predation, including by goshawks (*Accipiter gentilis*), sparrowhawks (*Accipiter nisus*), and hawk owls (*Surnia ulula*) [45]; predator vigilance has been identified as an adaptive response that contributes to the maintenance of stable

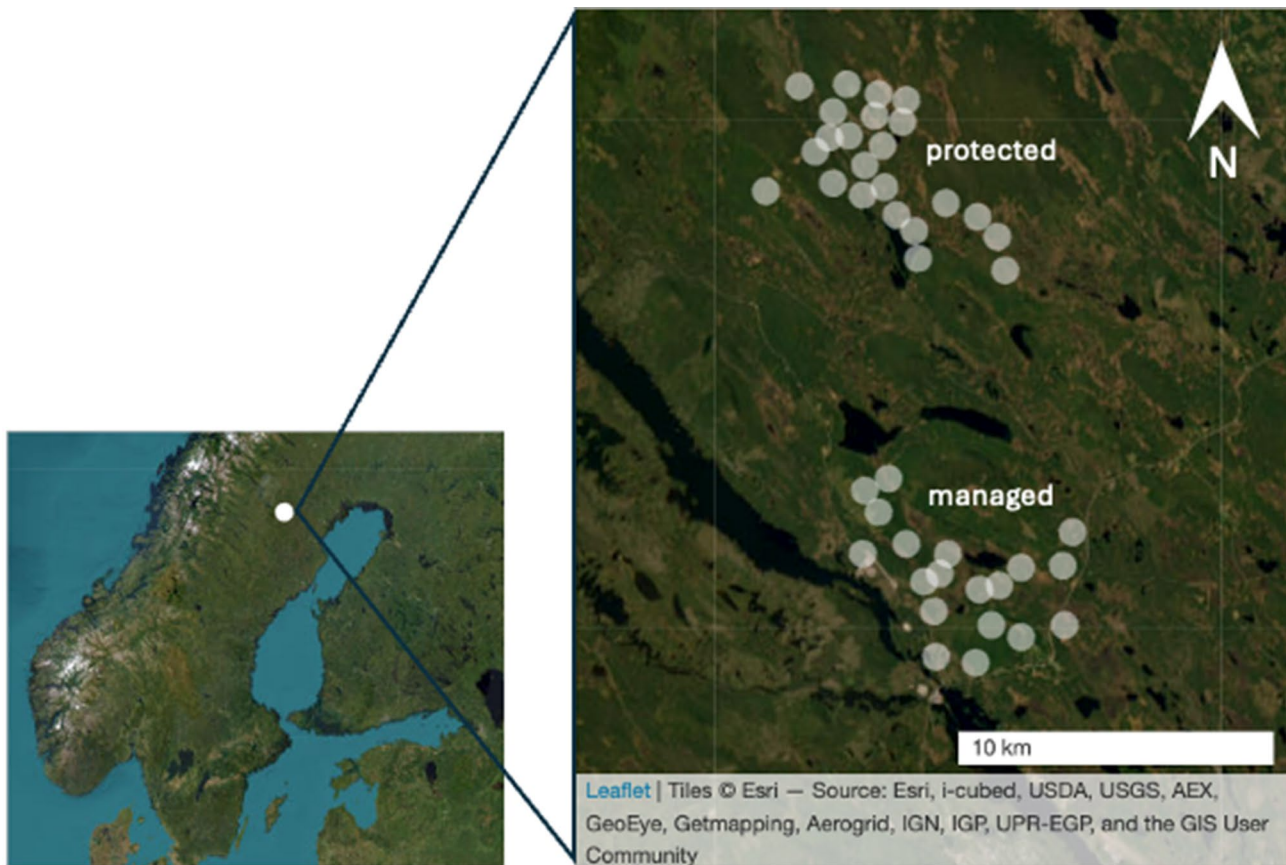


Fig. 1 Map showing the locations of the territories in the long-term Siberian jay study site in northern Sweden. The study population is found in protected (old-growth) and managed forests. Dots show locations of territories in this study. Map generated using the R package leaflet [51]. Map data copyrighted OpenStreetMap contributors and available from www.openstreetmap.org [52]

territorial groups [45]. Studies in the closely related, and ecologically equivalent, Canada jay (*Perisoreus canadensis*) suggest that the potential for pilfering among group members, independent of kinship, may also underlie group living in these birds [46–49]. In Siberian jays, cache pilfering among group members has been found to occur regardless of kinship [50], although this has yet not been explored as a potential mechanism underlying their territorial group structure.

The strong evidence for environmental factors driving microbiome composition in avian gut microbiomes [23] leads us to expect temporal and spatial patterns in the Siberian jay microbiome due to seasonal changes in habitat structure and diet. In the presence of a differential distribution of resources between territories, we may expect to detect area- and/or group-level convergences linked to geographical variation. Conversely, the lack of physical contact between group members (which is limited to pair and offspring provisioning during the breeding season) reduces opportunities for social structuring of the gut microbiome. Since higher alpha diversity (richness) is commonly assumed to be a healthier microbiome state

as it increases resilience and redundancy [53–55], we also hypothesize that alpha diversity is lower in individuals in the managed area. Similarly, we expect breeders, who are socially dominant over same-sex non-breeders and thus occupy a more optimal social status, to have higher alpha diversity than non-breeders.

Methods

Siberian Jay capture and sampling

All bird handling and sampling were conducted under ethics licence no. A23-20 of the Umeå University ethics committee; birds were ringed under licence no. 675 of the Swedish Museum of Natural History, Stockholm. Microbiome samples were collected from individuals from a population of individually colour-ringed Siberian jays outside Arvidsjaur, in Sápmi (65°40'N, 19°0'E; northern Sweden). Birds were caught using mist nets and placed in bags. We opportunistically collected samples from spontaneous defecation during handling and processing. Cloacal swabbing was performed by inserting a sterile swab (Puritan PurFlock swab, USA) approximately 4 mm into the cloaca. Faecal ($n=29$) and cloacal samples ($n=53$) were placed in DESS (DMSO/EDTA/saturated

saline) buffer, stored at -20°C upon return from the field at the end of the day, then at -80°C for long-term storage following transport on dry ice. We collected a total of 82 samples from 73 individuals over the course of four sampling seasons: Winter 2022 (March, $n=12$), Summer 2022 (June to July, $n=8$), Fall 2022 (August to October, $n=49$), and Winter 2023 (March, $n=13$). We collected samples in both protected and managed areas ($n=48$ and 34 , respectively). Age, where not previously known, was determined based on the shape of tail feather tips (adults $n=47$; juveniles $n=35$) and breeding status was recorded (breeders $n=31$, non-breeders $n=50$, unknown = 1) (SI Table 1).

DNA extractions, sequencing, and quality control

DNA extractions and sequencing were performed at the McMaster Genomics Facility (Hamilton, ON, Canada) following a modified version of the protocol described in [56]. Briefly, the V4 region of the 16 S rRNA gene was amplified using 515 F and 806R primers, generating 2×300 bp paired-end reads. Sequencing was performed on the Illumina MiSeq platform as described in [57]. Cutadapt was used to filter and trim adapter sequences and primers from the raw reads, with a minimum quality score of 30 and a minimum read length of 100 bp [58]. Amplicon sequence variants (ASVs) were filtered and trimmed based on the quality of the reads, error rates were learned, and ASVs were called using DADA2. Bimeras and ASVs identified in negative controls were removed, and taxonomy was assigned using the RDP classifier against the SILVA database version 1.3.8 [59]. Mitochondrial and chloroplast sequences were removed, as were dataset-wide singletons.

Statistical analyses

All analyses were conducted in the R statistical environment version 4.4.2 [60] primarily using the packages phyloseq (v. 1.50.0) [61] and vegan (v. 2.6.8) [62]. We identified dominant taxa using the package fantaxtic (v. 0.2.1) [63] and plotted our results using ggplot2 (v. 3.5.1) [64].

We used a non-parametric Kruskal-Wallis (KW) test to assess alpha diversity using two measures (Observed ASVs and Shannon index) against the following predictor variables: sampling season (Winter 2022/Summer 2022/Fall 2022/Winter 2023), area (managed/protected), age (adult/juvenile), sample type (faecal/cloacal), and breeding status (breeder/non-breeder/unknown). We used pairwise Wilcoxon signed-rank tests with a Bonferroni correction to identify pairwise differences.

We tested interindividual differences in microbiome composition (beta diversity) using distance-based redundancy analyses (db-RDA) using the function capscale from the package vegan, with ASV relative abundances as

the response matrix and based on 999 permutations. We transformed ASV relative abundances with the robust Aitchison method, as its centre log ratio (clr) transformation is specifically appropriate for microbial community data, which is sparse and can include many rare taxa [65]. We tested predictor variables independently (temporal principal coordinates of neighbourhood matrix (PCNM), sampling season, sample type, spatial PCNM, area, territory, age, breeding status, and individual identity). We performed stepwise model selection using the function ordi2step from the vegan package, which starts from a null model and adds variables until model fit is no longer significantly improved.

We used the aldex function from the package ALDEx2 (v. 1.38.0) [66] on clr-transformed values to perform differential abundance analyses and extracted Benjamini-Hochberg-corrected p -values of the Wilcoxon test. Lastly, we used the package microbiome (v. 1.28.0) [67] to investigate the common core microbiome, identifying genera present at high prevalences and relative abundances with a minimum threshold prevalence of 75% of samples.

Results

After quality filtering and sequence alignment, we obtained 3,748,491 reads corresponding to 3331 ASVs. Samples comprised, on average, 45,713 reads ($\pm 62,899$ standard deviation; maximum = 401,095; minimum = 37) and 88 ASVs (± 78 SD; maximum = 405; minimum = 8). In line with general avian gut microbiome findings [23], the dominant phyla by proportion of sequences (relative abundance) were Proteobacteria (61% of ASVs) and Firmicutes (28%) and individuals displayed a high degree of variation (Fig. 2A).

Alpha diversity

Alpha diversity differed significantly between seasons when measured in Observed ASVs (KW test, $\chi^2=9.71$, $p=0.021$) though not Shannon index (KW test, $\chi^2=4.45$, $p=0.22$) (Fig. 2B, SI Fig. 1). In Observed ASVs, Winter 2022 was significantly different from Fall 2022 and Winter 2023 (Wilcoxon test, $p=0.032$ and 0.012 , respectively) (Fig. 2B). Neither area, breeding status, nor age were significant predictors of either Observed ASVs or Shannon index (area: KW test, $\chi^2=1.01$, $p=0.31$ and $\chi^2=0.42$, $p=0.52$, respectively; breeding status: $\chi^2=1.48$, $p=0.22$ and $\chi^2=0.085$, $p=0.77$, respectively; age: KW test, $\chi^2=0.606$, $p=0.44$ and $\chi^2=0.37$, $p=0.55$, respectively) (SI Fig. 1). Sample type was significantly different in Observed ASVs (KW test, $\chi^2=6.96$, $p=0.008$) but not Shannon index (KW test, $\chi^2=1.39$, $p=0.24$), although this difference was in fact driven by season; within Fall 2022, which had both types of samples, there was no difference in sample type (KW test, $\chi^2=2.92$, $p=0.089$).

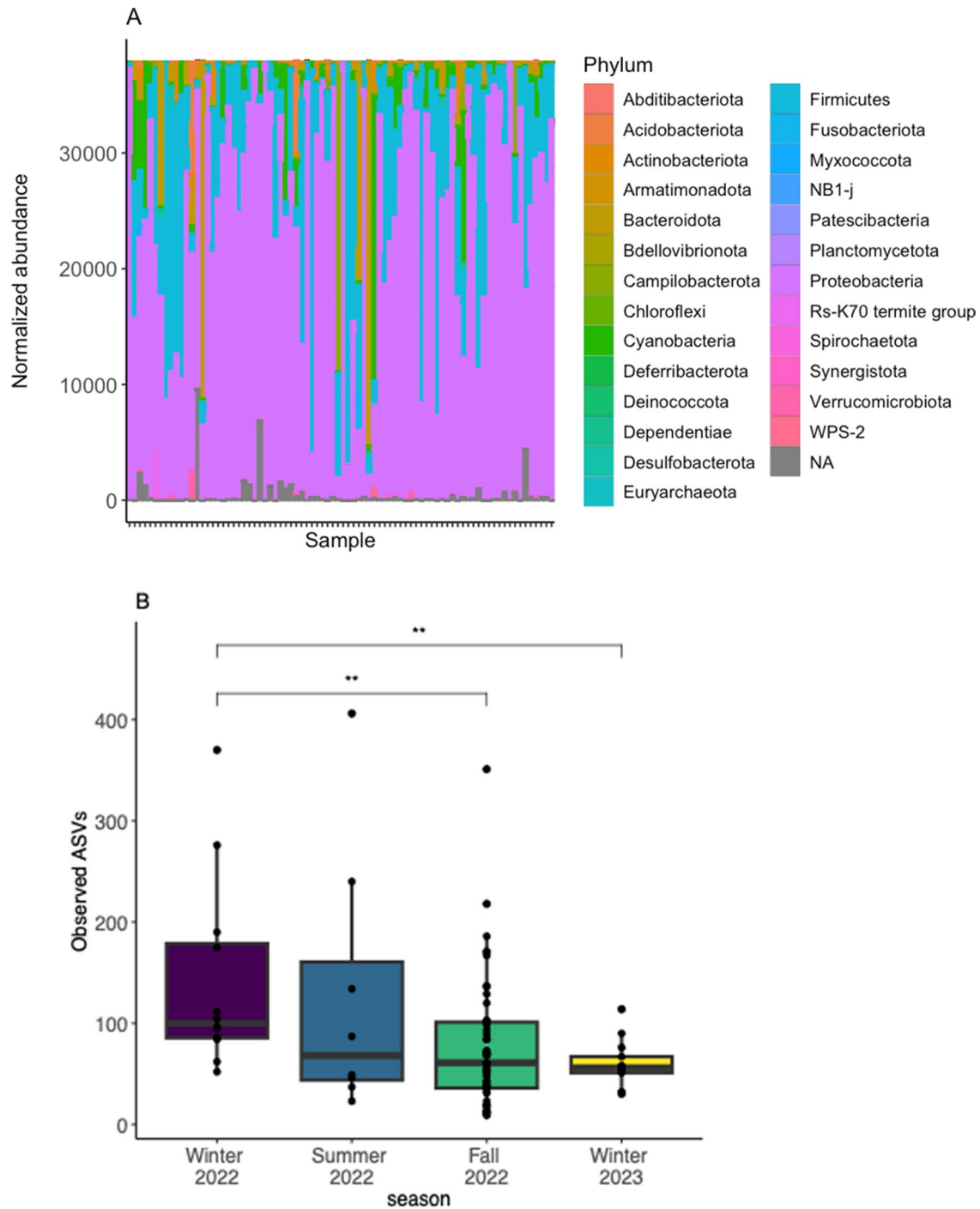


Fig. 2 Phylum-level relative abundances (A) and alpha diversity (B) of the gut microbiome of Siberian jays (Winter 2022 $n=12$, Summer 2022 $n=8$, Fall 2022 $n=49$, Winter 2023 $n=13$). Measured in Observed amplicon sequence variants (ASVs), alpha diversity only differed significantly between Winter 2022 and Fall 2022, and Winter 2022 and Winter 2023 (Wilcoxon test, $p=0.032$ and 0.012 , respectively)

Beta diversity

We first independently tested predictors of community composition (temporal PCNM, sampling season, sample type, spatial PCNM, area, territory, age, breeding status, and individual identity), then used model selection on all significant variables to reduce redundancy due to

collinearity [68]. Sampling season, sample type, age, and breeding status were significant; temporal PCNM, spatial PCNM, area, territory, and individual identity were not (SI Table 2). Our final model included sampling season, sample type, age, and breeding status. Stepwise model selection, based on forward addition of variables and

adjusted R^2 , identified season as the strongest and sole predictor of microbiome composition (db-RDA, $F = 2.13$, $\text{adj. } R^2 = 0.040$, $p = 0.001$, based on 999 permutations; Fig. 3A). We note that sample type was entirely confounded

by season, and within seasons, was not significantly different, as has been found in other bird species [69].

We performed a differential abundance analysis to compare Fall 2022 and Winter 2023 (we did not include Summer 2022 due to sample size considerations), which

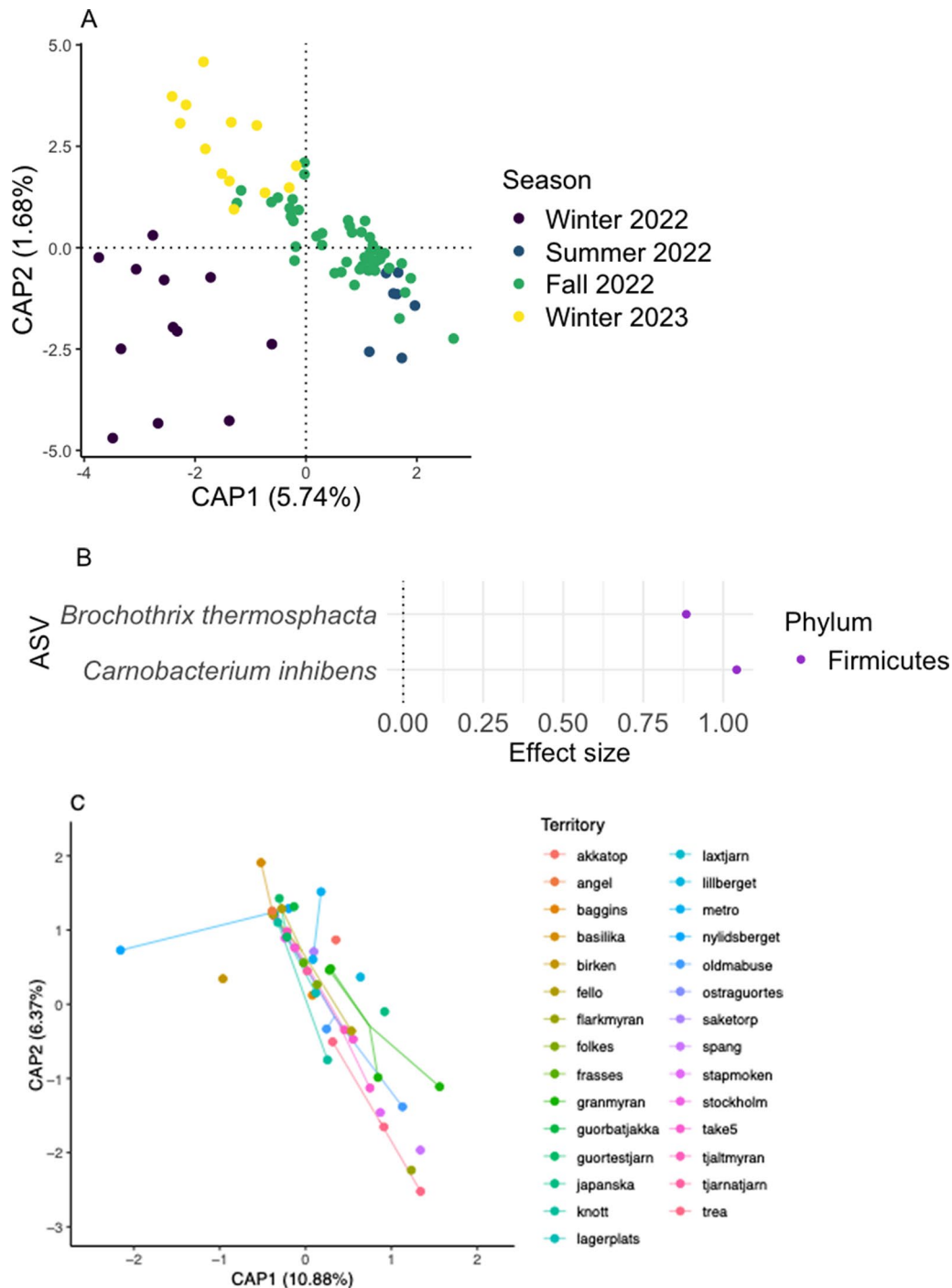


Fig. 3 Drivers of variation in the gut microbiome of Siberian jays. **(A)** Microbiomes varied seasonally; axes represent the first and second constrained axes from a Canonical Analysis of Principal Coordinates (CAP) (db-RDA, $F = 2.13$, $\text{adj. } R^2 = 0.040$, $p = 0.001$). **(B)** Two amplicon sequence variants (ASVs) were identified as more abundant in Winter 2022 than in Fall 2022. **(C)** Within Fall 2022, territory was a significant predictor of microbiome composition (db-RDA, $F = 1.34$, $\text{adj. } R^2 = 0.17$, $p = 0.031$)

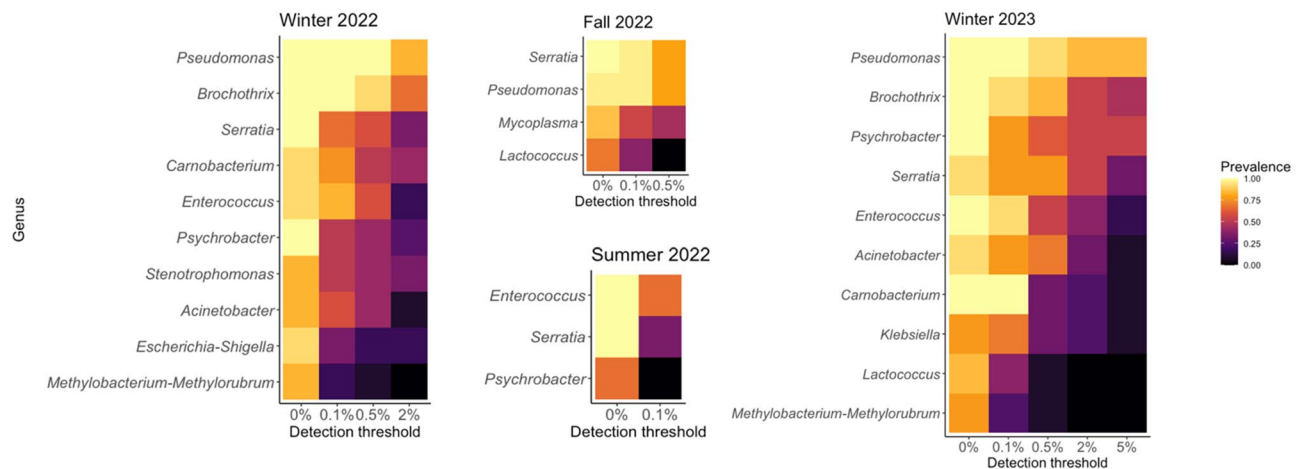


Fig. 4 Core genera found in four sampling seasons. Genera were considered core if they were found at higher relative abundances (detection threshold) in at least 75% of samples (prevalence)

identified *Brochothrix thermosphacta* and *Carnobacterium inhibens* as significantly enriched in Winter 2023 (Benjamini-Hochberg corrected Welch's t-test; *Carnobacterium inhibens* effect = 1.04, adj. $p = 0.0505$; *Brochothrix thermosphacta* effect = 0.88, adj. $p = 0.053$) (Fig. 3B). A differential abundance analysis between Winter 2022 and Winter 2023 did not identify any significantly differently abundant ASVs. We note that classification at the species level is not always reliable when using 16 S metabarcoding, and that species-level identification should be taken with caution.

In light of the seasonality in microbiome profiles, we repeated the beta diversity analysis on Fall 2022 samples—the only season with an appropriate sample size—to explore the drivers of variation within a season. Since the Fall 2022 cohort included one individual who was sampled twice, we restricted our analysis to 48 unique individuals. Within Fall 2022, only territory was a significant predictor (db-RDA, $F = 1.34$, adj. $R^2 = 0.17$, $p = 0.031$, based on 999 permutations) (Fig. 3C); temporal PCNM, sample type, spatial PCNM, area, age, breeding status, and individual identity were not (SI Table 2).

Core microbiome and differential abundance

We divided core microbiome analyses by season to determine whether, despite seasonal variation, any core taxa were retained (Fig. 4). *Pseudomonas* and *Serratia* were found at high relative abundances and prevalences across all seasons. Winter 2022 and Winter 2023 presented a noticeable overlap, with *Pseudomonas*, *Brochothrix*, *Serratia*, *Carnobacterium*, *Enterococcus*, *Psychrobacter*, *Acinetobacter*, and *Methylobacterium-Methylorubrum* found in both periods. A comparison between the two winter seasons did not identify a significant difference (db-RDA, $F = 1.08$, $p = 0.223$, based on 999 permutations).

Discussion

Concordant with our hypothesis, we found evidence and indication of environmental factors driving gut microbiome composition in Siberian jays, with significant temporal—but not spatial—patterns. However, contrary to our other hypotheses, we found an unexpected link between social structure and microbiome composition, but no association between alpha diversity and habitat type or social status. Overall, several correlative lines of evidence from our results suggest that passive environmental uptake is an important factor driving gut microbiome assembly in Siberian jays. First, microbial taxa that are prevalent in the local environment also dominate the gut microbiome of Siberian jays, as detailed below. Second, we observed significant temporal variation in both microbiome composition and richness, which may be tied to seasonal changes in habitat. Third, microbiome convergence within territorial groups likely reflects the horizontal transmission of environmental microbes among group members.

Our first line of evidence for environmental uptake concerns two ASVs, belonging to the genera *Pseudomonas* and *Serratia*, which were consistently present in relatively high abundance across all seasons (Fig. 4). We found that the *Pseudomonas* and *Serratia* ASVs identified in the Siberian jay gut match taxa found in the local bryophyte community [70, 71]. Indeed, unrelated investigations into the moss microbiome in precisely the same location as the protected area of our study site found both taxa to be prominent members of the bryophyte microbial community, a match made possible via the interactive ASV sequence function in the Microbe Atlas Project [72]. Given their relatively high abundance in the local environment, these taxa may be taken up by Siberian jays through environmental horizontal transmission while foraging on the ground, i.e., for berries or carrion.

Serratia may also be introduced into the Siberian jay gastrointestinal tract via direct dietary uptake, as it is a common gut symbiont of insects [73–76] and may be present in those consumed by Siberian jays. The occurrence of *Serratia* in insect guts has itself been attributed to environmental uptake [73, 76]; a similar mechanism may also underlie their presence in the Siberian jay gut. While it is essential to keep in mind that this interpretation is based on correlational evidence, it aligns with previous work suggesting that environmental microbes play an important role in shaping birds' gut microbiomes [39, 77].

The strong seasonal component to microbiome composition (Fig. 3A) also supports the notion that microbiome assembly in Siberian jays is strongly influenced by changing environmental factors. The temporal variation in microbiomes may correspond to changes in the local microbial species pool, which varies over the course of the year as the environment goes from snow-covered to vegetated, and the jay diet shifts from cached food to grubs to berries. Seasonal patterns in core and differential abundance analyses (Figs. 3B and 4) also suggest environmental uptake of microbial taxa associated with seasonal patterns in resource availability or, possibly, seasonal temperature differences [78]. Despite large shifts over the year, differences in composition from the two winter subsets were less pronounced than between other seasons, with no differentially abundant taxa and overlapping core taxa. We also found significant seasonal variation in microbial species richness (observed ASVs), although not once species evenness was taken into account (Shannon index) (Fig. 2B, SI Fig. 1). Nevertheless, given the correlative nature of our findings, we cannot exclude that seasonality in physiological demands may be driving the temporal pattern we observed in the Siberian jay gut microbiome.

Similar seasonal patterns have been observed in the oral microbiome of Canada jays, the Siberian jay's North American congener, where they are attributed to seasonal changes in the environmental microbial species pool [79]. Canada jays occupy the same niche as Siberian jays: they are group-living, year-long residents of the boreal forest who survive on food caches scattered throughout their territory. The mechanisms that govern microbiome assembly in Canada jays are likely similar to those in Siberian jays. In fact, the core microbiomes of the Siberian jay gut microbiome share several taxa with the core oral microbiome of Canada jays. In both species, *Pseudomonas* is the dominant genus, while *Lactococcus*, *Escherichia-Shigella*, and *Carnobacterium* are also common to both [79]. The similarity between oral and gut microbiomes in both species suggests that in *Perisoreus spp.*, ingestion of microbes may passively constitute the gut microbiome via an environment–oral–gut route for microbial community assembly.

Seasonal patterns in the gut microbiome of Siberian jays are further supported by the differential abundance analysis between Fall 2022 and Winter 2023. Two ASVs were more abundant in winter (*Brochothrix thermosphacta* and *Carnobacterium inhibens*), both of which are associated with the decay of animal substances [80]. It is possible that these taxa are found at higher abundances during the winter, when decaying meat from caches and carcasses comprises a larger part of the Siberian jay diet [42]. Additionally, several taxa found in the winter core Siberian jay microbiomes have been identified in the guts of carrion-eating insects, including *Carnobacterium*, *Brochothrix*, and *Acinetobacter* in several species of necrophagous vulture bees (family Apidae) [81], and *Pseudomonas*, *Serratia*, and *Psychrobacter* in burying beetles (*Nicrophorus spp.*, *Oiceoptoma noveboracense*, *Necrophila americana*) [76, 82]. Similar to our proposed mechanism in Siberian jays, microbiome assembly in burying beetles is thought to occur by passive environmental uptake of bacteria found on carcasses [82].

That said, we cannot rule out that Siberian jay gut microbes, even if acquired environmentally, are nevertheless symbiotic and play a functional role within their hosts. A promising future avenue lies in identifying the relative occurrence of environmental vs. symbiotic microbes in the Siberian jay gut. Additional longitudinal data on this population would be valuable, as would investigating geographically varied populations to test whether the Siberian jay microbiome tends to match that of the local environment or, rather, whether it is consistent across populations. Lastly, uncovering microbial function through meta-omics, in addition to conducting taxonomic inventories, is a promising avenue for future research.

Our results also present unexpected evidence of social structuring of the gut microbiome in a wild bird outside of the breeding season. In wild social mammals, allogrooming, fluid exchange, and close physical proximity can result in social structuring of the microbiome [19, 20, 83]. However, here we found that the microbiome of Siberian jays is socially structured despite the absence of allopreening, allofeeding, and other social behaviours that require physical proximity [42], which are thought to underlie social effects on microbiomes in other bird species [33, 34, 36]. A purely spatial effect at the scale of individual territories can be discounted: we did not detect any spatial effects despite conducting a PCNM to account for a range of spatial patterns and scales. Dietary differences between groups are also an unlikely explanation for this pattern, as the jays' fall diet consists overwhelmingly of berries, which are widespread across the study site. This would suggest that a group-level—rather than geographical—process underlies the observed social convergence of the microbiome.

The social structuring of the gut microbiome in Siberian jays also supports an environment–oral–gut route for microbial community assembly: cache pilfering between group members likely drives the observed group-level convergence. When collecting food for caching, individuals form a compact bolus of food bound together with copious amounts of saliva, which contains their oral microbiome. A substantial amount of cached food items is then pilfered by other group members: a radioactive food labelling study in this population found that over six weeks, 33% of labelled food items were recovered by other group members [50]. This behaviour may facilitate the horizontal transfer of microbes among group members and drive group-level convergence. In the future, comparing the oral and gut microbiomes of Siberian jays at a high taxonomic resolution would enable us to identify whether ASVs are indeed shared between the start- and endpoints of their gastrointestinal tract.

Vertical transmission among related group members is unlikely in the periods covered by our study. Generally, bird gut microbiomes upon hatching are low in richness and parental provisioning is the main vertical transmission mechanism shaping early-life microbiome composition [84, 85]. In Siberian jays, parents provision their offspring from the nestling stage until four weeks post-fledging, a period that was not included in our sampling. Our observation of temporal—but not age-related—variation in microbiome variation suggests that in the fall, the microbiome of juveniles is likely shaped by similar environmental processes as that of adults, similar to what has been found in migratory bird species [39]. Group-level similarities in the fall are thus unlikely to be due to carry-over effects from parental provisioning earlier in the year. Nevertheless, this area is ripe for prospective research. Future work that includes breeding periods, kinship data, and cross-fostering experiments would enable us to parse the relative contributions of vertical and horizontal transmission to Siberian jay gut microbiome assembly.

We did not find any evidence of a correlation between habitat quality or breeding status and alpha diversity. However, our findings uncovered seasonal variation in alpha diversity, likely reflecting temporal dietary patterns and seasonal turnover of the local environmental microbial community. The common assumption that higher alpha diversity in host-associated microbiomes is a more optimal state [53–55] may, therefore, need to be revised for studies in wild animals. Furthermore, in populations where passive processes underpin microbiome assembly, measuring microbial species richness may have only limited value.

Conclusions

Large seasonal shifts suggest that the host–microbiome association in Siberian jays is potentially weaker than in systems that exhibit more robustness to seasonal changes. Our findings are characterized by high variation in individual microbiomes despite generally low richness and a similarity to the local environmental microbial pool. The composition of the gut microbiome of Siberian jays appears to be driven by seasonality in environmental and food-derived inocula, while indirect exchange of microbes via reciprocal pilfering of food caches likely drives group-level homogenization. Notably, we did not detect a core microbiome that was conserved across seasons. While these results suggest that environmental uptake processes drive the assembly of the gut microbiome in Siberian jays, their gut bacteria may nevertheless play functional roles. Future investigations combining long-term, repeated sampling with metatranscriptomic and metaproteomic analyses are necessary to further understand if—or to what extent—the gut microbiome has an adaptive value in Siberian jays.

Supplementary Information

The online version contains supplementary material available at <https://doi.org/10.1186/s42523-025-00496-8>.

Supplementary Material 1

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Author contributions

ELT collected data, conducted the analyses, prepared the figures, and wrote the manuscript text. AM and SL collected data and provided editorial feedback. KC funded sequencing work and provided editorial feedback. MG funded fieldwork and provided editorial feedback. KC and MG contributed equally. All authors read and approved the final manuscript.

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Data availability

All script files and metadata used in these analyses are available in a dedicated GitHub repository (<https://github.com/elephant/siberian-jay-gut-microbiome>). Sequencing data can be found under SRA BioProject PRJNA1198107.

Declarations

Ethical approval

All bird handling and sampling were conducted under ethics licence no. A23-20 from the Umeå University ethics committee. Birds were ringed under licence no. 675 from the Swedish Museum of Natural History, Stockholm.

Consent for publication

Not applicable.

Competing interests

The authors declare no competing interests.

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