

ARTICLE

Diversity of vector-dispersed microbes peaks at a landscape-defined intermediate rate of dispersal

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Abstract

Dispersal has long been recognized as a primary determinant of species diversity in ecological communities. This knowledge is mostly built on studies of organisms that disperse actively by themselves or passively via physical forces. For organisms that disperse passively via other organisms, the landscape characteristics that affect their vectors should indirectly influence the diversity of the vectored, but these relationships remain poorly understood. We investigated landscape–dispersal–diversity relationships in nectar-inhabiting bacteria that disperse via flower-visiting insects. Field observations and experiments revealed that bacterial diversity peaked at an intermediate frequency of insect visits, which was in turn determined by the surrounding landscape characteristics observed at the 200-m radius scale. Based on this finding, we discuss the possibility that the taxonomic diversity of vectored organisms tends to be maximized at an intermediate dispersal rate, especially in the widely observed situation where the vectored organisms and/or their habitat patches constitute consumable resources for their vectors.

KEYWORDS

dispersal–diversity relationship, flower-visiting insects, intermediate dispersal hypothesis, nectar bacteria, phoresy, pollination, vector-mediated dispersal

INTRODUCTION

Dispersal rate, or the rate at which individuals disperse from regional external sources to local habitat patches, has long been considered a primary factor shaping local biodiversity (MacArthur & Wilson, 1967). Theory and empirical evidence suggest that diversity is highest under an intermediate rate of dispersal. Specifically, as dispersal rate increases, the probability that not only new species but also dominant competitors colonize in local habitat

patches increases, eventually resulting in reduced diversity due to competitive exclusion (Cadotte, 2006; Mouquet & Loreau, 2003). However, whether diversity shows a hump-shaped relationship with dispersal rate as predicted or instead increases monotonically with dispersal rate (Loke & Chisholm, 2023; Loreau & Mouquet, 1999) can depend on the spatial scale of observation relative to that of local habitat patches (Lu et al., 2019). Furthermore, increasing attention has been paid to determinants of dispersal rate (Baguette

et al., 2013). Besides obvious differences among species that vary in their dispersal capacity, another consideration is the landscape context. Even the same type of organism can vary greatly in dispersal rate, depending on, for example, how permeable the landscape surrounding the focal habitat patch is to the dispersing organisms (Mony et al., 2020, 2022).

Many of these investigations into the relationship between dispersal, diversity, and landscape characteristics have assumed that dispersal happens either actively as organisms move by themselves or passively via such physical forces as wind, rain, and gravity (Loke & Chisholm, 2023; Vanschoenwinkel et al., 2013). For these organisms, the connectivity (e.g., distance) between the regional source pool and the local habitat patches largely determines dispersal rate (MacArthur & Wilson, 1967). However, a wide range of plants, animals, fungi, and bacteria disperse by hitchhiking on an organism of another species that moves a longer distance than they do themselves, the mode of dispersal known as phoresy (Bartlow & Agosta, 2021). Examples include ungulate-dispersed grasses (Plue & Cousins, 2018), bird-dispersed fishes (Lovas-Kiss et al., 2020), rodent-dispersed fungi (Borgmann-Winter et al., 2023), and fly-dispersed bacteria (Wohlfahrt et al., 2020), to name just a few (Bartlow & Agosta, 2021). One characteristic commonly shared across many of these phoretic species is that they are not just dispersed but consumed by their vectors as well. For these species that are carried (and consumed) by dispersal vectors, the landscape matrix affecting the movement of the vectors, rather than the vectored, influences dispersal rate and, consequently, diversity. Thus, to understand landscape–dispersal–diversity relationships more comprehensively, the effects of vector-mediated dispersal should be studied in a landscape context. Yet, few empirical studies have addressed these relationships in phoretic organisms.

In this paper, we report the results of a field study that examined how landscape matrix indirectly shapes the diversity of vector-dispersed organisms by affecting their vectors. Specifically, we focus on bacteria that inhabit floral nectar, which has been increasingly used as a natural microcosm (*sensu* Srivastava et al., 2004, 2026) to address fundamental questions in population and community ecology over the past decade (Chappell & Fukami, 2018). These bacteria rely mainly on flower-visiting insects to disperse among flowers (Cusumano et al., 2023; Herrera et al., 2008; Vannette & Fukami, 2017). We first sought to identify the characteristics of the surrounding landscape that affected the frequency of insect visits to flowers. Building on this analysis, we then investigated the relationship between the rate of insect-mediated bacterial dispersal and the

diversity of bacterial taxa through a complementary pair of field observation and experiment. Both observational and experimental data revealed hump-shaped responses of bacterial diversity to the rate of insect-mediated dispersal as determined by landscape matrix. Informed by these findings, we discuss the possibility that this intermediate dispersal pattern is commonly observed in many systems where the vectored organisms, their habitat patches, or both constitute consumable resources for their dispersal vectors.

MATERIALS AND METHODS

Study system

This study was conducted in September 2020 in agricultural fields of buckwheat (*Fagopyrum esculentum*) embedded in a rural landscape consisting of a small-scale mosaic of agricultural fields, woodlands, grasslands, riparian zones, and residential areas in the town of Iijima in Nagano Prefecture, located in central Japan (Figure 1A–C, 35°67'67" N, 137°91'96" E). In this region, buckwheat is cultivated with the same amounts of seeds sown (0.4–0.5 kg/a) and fertilizers applied (100 kg/a) across hundreds of small fields (many are less than 0.5 ha), making the fields comparable among one another in these respects. No agrochemicals (e.g., pesticides, herbicides, fungicides) are used during buckwheat cultivation.

Bacterial communities that form within floral nectar can be delineated clearly, with flowers on the plant and more broadly within agricultural fields forming metacommunities in a spatially hierarchical fashion (Chappell & Fukami, 2018; Rering et al., 2024). Furthermore, the dispersal vectors of nectar-inhabiting bacteria, that is, flower-visiting insects, are diverse in buckwheat, with microbial dispersal rate varying with insect abundance (Figure 1C, Miyashita et al., 2023; Nagano et al., 2021). Previous work in this landscape (Miyashita et al., 2023) and elsewhere in Japan (Taki et al., 2010) has shown that the frequency of flower visits by pollinators is determined by the landscape matrix of buckwheat fields. Specifically, from previous work (Bartual et al., 2019), more insects are expected to visit buckwheat flowers when there are more forest edges in the landscape surrounding the field. These characteristics of bacteria in buckwheat nectar make them suitable for studying the effects of landscape matrix and vector-mediated dispersal on the diversity of the vectored organisms.

Nectar frequently contains yeasts in addition to bacteria, and these two groups can affect each other strongly within nectar (Álvarez-Pérez et al., 2019; Chappell et al., 2022; Tucker & Fukami, 2014). Our preliminary work

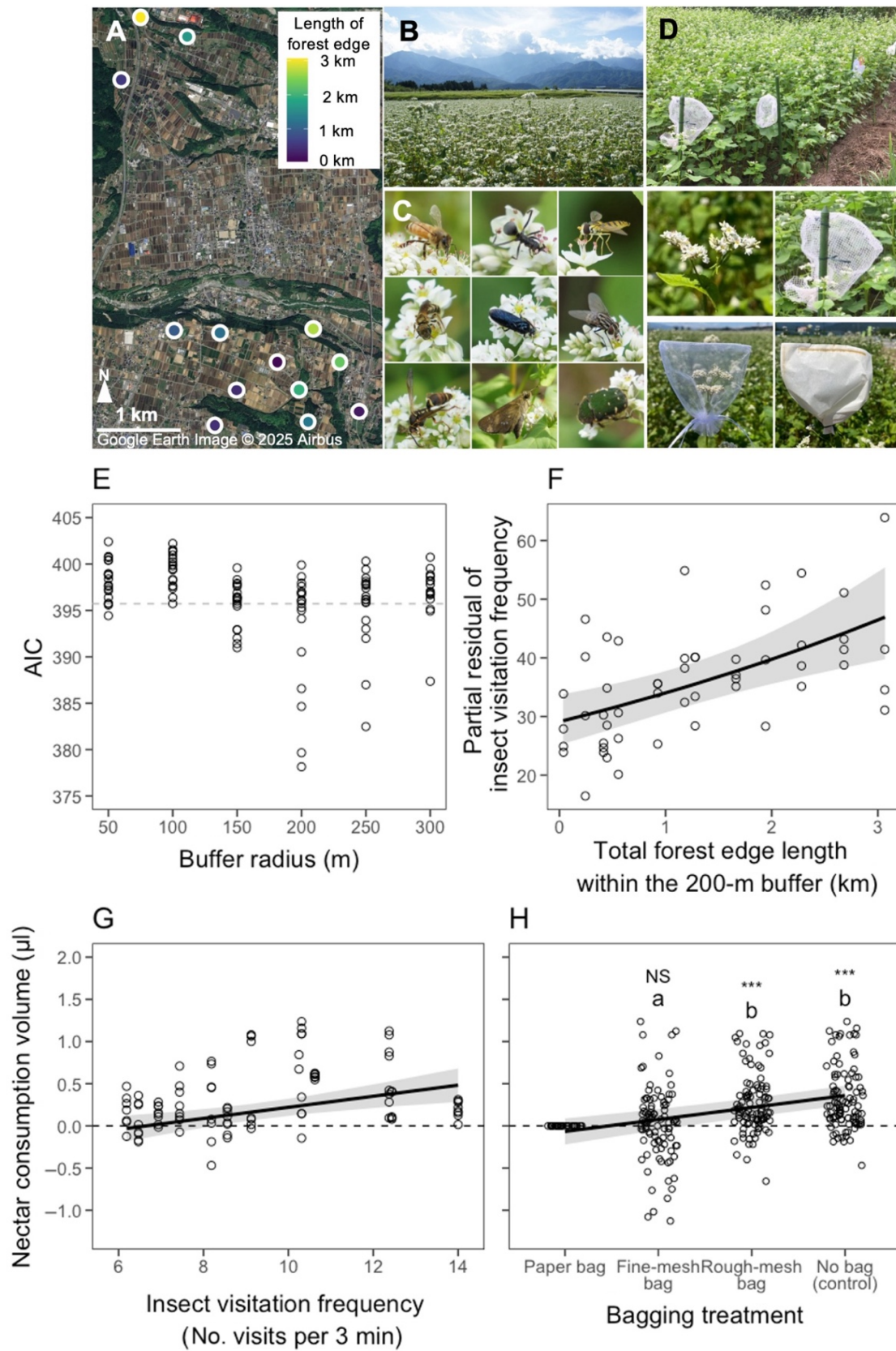


FIGURE 1 Legend on next page.

indicated, however, that buckwheat nectar in our study landscape had few yeasts and was predominantly inhabited by bacteria (see Appendix S1: Section S1). This overrepresentation of bacteria is commonly observed in plant species of short-lived flowers with short corollas (Vannette et al., 2021). Buckwheat flowers have short corollas, and most flowers last only a single day. For this reason, we focused on bacteria in this study.

Study site

We selected 13 buckwheat fields for this study. All selected fields were located at least 400 m away from the nearest-neighbor field used in this study (Figure 1A). In addition, the fields were chosen to minimize spatial bias among the fields in terms of forest edge length such that the fields having similar forest edge length would not be spatially aggregated (Figure 1A). The focus of this study was to understand how the characteristics of the landscape matrix surrounding a buckwheat field affected the foraging behavior of individual insects as microbial vectors. As such, this study differs from those that aim to understand how landscape characteristics influence the population dynamics of insects in the landscape (e.g., Eeraerts et al., 2019; Ekroos et al., 2013; Nicholson et al., 2017), which typically require observation at larger spatial scales than needed for the purpose of this study.

To quantify landscape matrix, we categorized human land use into four types: forest edges, buckwheat fields, other agricultural lands (e.g., paddy fields and orchards), and residential areas. To calculate the area of each land-use type, buffers of varying radii ranging from 50 to

300 m at 50-m intervals were generated from the edge of each field using GIS performed by R version 4.4.0 (R Core Team, 2024) and sf package (Pebesma, 2018). Previous reports indicate that a 100–300 m buffer radius best captures landscape characteristics for estimating the flower visitation frequency of insects, other than that of *Apis* and *Bombus* bees (Benjamin et al., 2013; Földesi et al., 2015; Steffan-Dewenter et al., 2002), which were rare in our study region in September (Miyashita et al., 2023; Nagano et al., 2021, 2025). The Shannon diversity index of land-use proportion was calculated as the landscape heterogeneity index. To characterize landscape matrix, forest edge length and landscape heterogeneity were used. For each field, we also recorded whether the field margins were mown or set-aside (i.e., experimentally left unmown from approximately 4 weeks before the start to buckwheat blooming until the beginning of buckwheat harvest), which can also influence the abundance of flower-visiting insects (Nagano et al., 2025). Vegetation height of wild plants in recently mowed field margins was less than 10 cm. Vegetation in set-aside field margins was taller than 30 cm.

Field observations

We used observational and experimental approaches as complementary methods to investigate the relationship between the frequency of insect visits to flowers and the taxonomic diversity of bacteria in nectar. For the observational approach, we quantified the frequency of flower visits by insects at each of the 13 buckwheat fields (Figure 1A). For this purpose, we established four

FIGURE 1 Study system, bagging methods, and the observed relationship between landscape characteristics and the frequency of insect visitation to buckwheat flowers. (A) Map showing the location of the 13 buckwheat fields used in this study. The color indicates the length of forest edge within the 200-m buffer, with brighter colors denoting longer forest edge lengths. (B) One of the buckwheat fields (photo by Yuta Nagano). (C) Some of the diverse insects that visit buckwheat flowers. From top-left to bottom-right photos, *Apis mellifera*, *Formica japonica*, *Sphaerophoria macrogaster*, *Halictus aerarius*, *Arge similis*, Sarcophagidae sp., *Polistes snelleni*, *Parnara guttata*, and *Gametis jucunda* (photos by Yuta Nagano). (D) Buckwheat inflorescences bagged for insect exclusion. The middle photos show no bag control, allowing access to all arthropods, and rough-mesh bag treatment (mesh size = 4.5 mm), allowing access only to arthropods smaller than 4.5 mm long, such as small hoverflies and ants. The bottom photos show fine-mesh bag treatment (mesh size = 0.4), allowing access to arthropods smaller than 0.4 mm long such as thrips and mites, and paper bag treatment, allowing access to no arthropods (photos by Yuta Nagano and Tadashi Fukami). (E) Results of Akaike information criterion (AIC) model selection, where each dot represents the AIC value of each model describing the relationship between landscape characteristics and insect visitation frequency. Gray dashed line indicates the AIC value of the null model. (F) Relationship between landscape characteristics (as quantified by forest edge length within the 200-m radius of the focal fields) and the frequency of insect visitation to buckwheat flowers in a field. Data points represent four observations at each of the 13 study fields, with the predicted mean and 95% CI. (G) Estimated relationships between nectar consumption volume and insect visitation (mean number of insect visits observed per 3 min in a 1 × 10 m transect) ($R^2 = 0.38$, $p < 0.001$). (H) Effect of bagging treatment on nectar consumption volume. Different letters indicate significant difference ($p < 0.05$). Nectar consumption volume was calculated as the difference in nectar volume from flowers with the paper bag treatment. NS ($p > 0.05$) and *** ($p < 0.001$) indicate the results of a t test that tested whether the mean nectar consumption volume was larger than zero. The shaded range of estimates indicates 95% CI. Detailed statistics are shown in Appendix S2: Tables S5–S7.

transects (1×30 m), with one transect placed along each of the four sides of the fields in most cases. In each observational transect, insects visiting buckwheat flowers were observed between 9:00 a.m. and 11:50 a.m. on four sunny days, on September 9, 14, 15, and 17 of 2020. This data collection involved walking along the field margin for 3 min per observation, following Miyashita et al.'s (2023) methods. Insect visitation frequency was recorded separately for 10 insect groups: honeybees, wild bees, ants, wasps, sawflies, hoverflies, other flies, butterflies, flower chafers, and other beetles (Figure 1C, Nagano et al., 2025).

To quantify bacterial abundance and diversity in floral nectar, we established four sites at each of the 13 buckwheat fields (Figure 1A), with one site placed along each of the four sides of the field in most cases. At each site, we sampled nectar from two plants of different floral morphs, one pin and one thrum (Cawoy et al., 2006). From each plant, we collected nectar from four flowers on an inflorescence in the late afternoon between 4:00 p.m. and 5:00 p.m. on September 5, 8, 9, and 11–13 of 2020. Nectar was collected using a 0.5- μ L microcapillary tube. The nectar from the four flowers was consolidated to make one sample. The total volume of each of these nectar samples was measured, and each sample was immediately placed into a separate PCR tube containing 40 μ L of distilled water. The diluted samples were kept cool in a Styrofoam box with ice packs until transported to the laboratory. Within 2 h of the sampling in the field, 5 μ L of each diluted sample was then diluted further in the laboratory and plated onto tryptic soy agar (TSA; 1.5% tryptone, 0.5% soytone, 0.5% NaCl, 5% fructose, 1.5% agar, all (w/v)) plates with the antifungal cycloheximide to obtain CFU (colony-forming units) counts. We used the CFU counts as an estimate of bacterial abundance in nectar, which should be interpreted with caution as not all bacterial taxa may form colonies on any given media. However, many of the dominant bacteria taxa in floral nectar, such as species of *Acinetobacter*, *Rosenbergiella*, *Erwinia*, *Pantoea*, *Pseudomonas*, and *Sphingomonas* are culturable on TSA (Quevedo-Caraballo et al., 2025; Vannette et al., 2021). CFUs were counted after 2 days of incubation at room temperature (about 20–26°C). The remainder of the original samples were stored at -80°C until used for DNA extraction and PCR for metabarcoding (Appendix S1: Section S2). The observed number of amplicon sequence variants clustered with a 97% sequence similarity threshold (ASV₉₇) for all nectar samples was within the range of saturation with respect to the read number, even when all singletons were retained in the data (Appendix S2: Figure S1).

Field experiments

For the experimental approach to examine the relationship between insect visitation frequency and nectar bacterial diversity, we established four experimental blocks at each of the 13 buckwheat fields (Figure 1A). In most fields, we had one block along each of the four sides of the field. In each experimental block, we had two sets of the following three inflorescence treatments: an inflorescence covered with a fine-mesh bag (0.4 mm), an inflorescence covered with a rough-mesh bag (4.5 mm), and an inflorescence without a bag (control) (Figure 1D). We chose a pair of plants with different floral morphs for each treatment. The control inflorescences were the same as those used for the field observation. In addition, in one of the four experimental blocks in each field, we had a fourth treatment, which was two inflorescences (one pin and one thrum) each covered with a paper fruit bag. The bagging was used to prevent insects of differing sizes from visiting the flowers on the bagged inflorescences. The paper bag, the fine-mesh bag, and the rough-mesh bag were intended to exclude all arthropods, allow only arthropods smaller than 0.4 mm long (e.g., thrips and mites), and allow only arthropods smaller than 4.5 mm long (e.g., small hoverflies and ants), respectively. The bagging was done between 8:00 a.m. and 10:00 a.m. (Figure 1D). Nectar collection, plating, DNA extraction, and PCR for metabarcoding were done following the same methods as for the field observation (Appendix S1: Section S2). As usual with any other systems, reduced diversity may sometimes represent reduction in population size below the detection threshold rather than true extinction.

The bagging treatment was used to experimentally create a gradient of insect visitation frequency, with no-bag treatment allowing for the highest frequency, followed by rough-bag, fine-bag, and paper-bag treatments in that order. The bagging treatment also caused changes in the types of insects visiting flowers, in addition to altering overall visitation frequency. Although these effects can complicate interpretation of the experimental results, we found no significant difference in bacterial taxonomic composition among the four bagging treatments (Appendix S2: Figure S2, PERMANOVA, $p = 0.996$), suggesting that no significant difference existed in the taxonomic identity of bacterial taxa vectored by insects of different sizes (see also Appendix S2: Figure S3). Therefore, in our system, any difference in bacterial diversity we observed among the bagging treatments could be attributed mainly to insect visitation frequency rather than to insect species identity.

Statistical analysis

We first checked for spatial autocorrelation for insect visit frequency among fields, based on Moran's I statistics (Cliff & Ord, 1973). As we found no significant autocorrelation ($I = -0.16$, $p = 0.69$), spatial autocorrelation was not included in subsequent analyses.

The effects of landscape matrix on insect visitation frequency were analyzed using generalized linear mixed models (GLMMs). The response variable was insect visitation frequency, and explanatory variables were forest edge length, landscape heterogeneity, field margin management, and two-way interaction terms (forest edge length $\times$ landscape heterogeneity, forest edge length $\times$ field margin management, and landscape heterogeneity $\times$ field margin management). A negative binomial distribution was used for the error term, and the field identity and observing date were included as random terms. To detect effective variables and spatial scales, we performed model selection based on the Akaike information criterion (AIC) for all possible models with combinations of explanatory variables and spatial scales (171 models = 17 combinations of explanatory variables $\times$ 10 buffer radius sizes + null model). Effective variables in selected models were chosen based on the absolute z -value (estimated coefficient/SE) being greater than 2.0 (Burnham & Anderson, 2002). Correlation coefficients between variables were never very large ($|r| < 0.58$), indicating no severe collinearity.

To examine the relationship between nectar consumption volume and insect visitation frequency and to examine differences in nectar consumption volume among bagging treatments, linear mixed model (LMM) and analysis of variance (ANOVA) were used, respectively. Nectar consumption volume was calculated as the difference in nectar volume that was collected from the same flower morphs (pin or thrum) and in the same fields and date between the paper bag treatment and the other bag treatments (no, fine-mesh, and rough-mesh bag treatments). In LMM, nectar consumption volume was used as the response variable, and explanatory variables included insect visit frequency, insect diversity calculated as the Simpson diversity index, and flower morphs (pin and thrum). Since thrum flowers tend to have more nectar than pin flowers (Cawoy et al., 2006), flower morphs were used as a covariate. The random terms were field identity and sampling date. Statistical significance of each explanatory variable was tested using the Wald test. In ANOVA, nectar consumption volume was used as the response variable, and bagging treatments, excluding the paper bag treatment, and flower morphs were used as fixed variables. The random terms were the same as for LMM above. Additionally, to cope

with heteroscedasticity among bagging treatments, variance parameters of each treatment were estimated in the same ANOVA model. If ANOVA indicated a significant difference among bagging treatments, that is, $p < 0.05$, multiple comparison was conducted using the Tukey–Kramer methods as a post hoc test. We determined whether nectar consumption volume was higher than zero using a t test of the population mean. Furthermore, we used an ordinal dummy variable of bagging treatment, which reflects insect visitation (paper bag = 1, fine-mesh bag = 2, rough-mesh bag = 3, and control = 4) and estimated a linear relationship between nectar consumption volume and bagging treatments using LMM.

To examine the relationship between insect visitation frequency and the number of bacterial ASV₉₇ and CFU, GLMs were conducted at flower and field scales. Response variables were the number of ASV₉₇ and the number of CFU. We log₁₀-transformed CFU for analysis. Explanatory variables were visitation frequency, the quadratic term of visitation frequency, and insect diversity. Error terms were the Poisson and Tweedie distributions for the number of ASV₉₇ and CFU, respectively. To cope with the large variation observed in the number of ASV₉₇ per flower and CFU per flower, which was likely caused by high stochasticity in the number of insect visits, we used the top 30% data points in each of 10 bins that were equally divided in the range of insect visitation frequency, following Turner and Montagna's (2016) methods. We focused on the top 30% data to deal with zero inflation, but we also conducted the same analysis using all data, which yielded qualitatively identical results (Appendix S1: Section S3; Appendix S2: Figure S4, Tables S1–S3). The statistical significance of each explanatory variable was tested using the Wald test. If the estimated coefficient of the quadratic term of visitation frequency was significantly negative, we conducted two additional analyses to determine whether ASV₉₇ (or CFU) had a hump-shaped relationship with insect visitation frequency. First, to investigate whether the linear and quadratic terms of insect visitation frequency significantly improved the explanatory power of the model, we used the likelihood ratio test and AIC to compare the above model with a model that excluded insect visitation frequency from the explanatory variables (hereafter null model). Second, we also tested whether the peak of the response variable existed within the observed range of insect visitation frequency by calculating the 95% CI of the optima using Fieller's theorem (Oksanen et al., 2001; ter Braak & Looman, 1986). Correlation coefficients between insect visitation frequency and insect diversity were not large ($r = -0.46$), indicating no serious collinearity.

The differences in the number of ASV₉₇ and the number of CFU among the bagging treatments were analyzed using ANOVA and GLMs. For analyses of ASV₉₇ and CFU per flower, we used the top 30% data points of each bagging treatment for the same reason as above. Response variables and error terms were the same as described above for the relationship with insect visitation frequency. For ANOVA, the fixed term was bagging treatments. If ANOVA indicated a significant difference among the bagging treatments, multiple comparisons were performed using the Tukey–Kramer method as a post hoc test. For GLMs, we used an ordinal dummy variable of bagging treatment. Both linear and quadratic terms of the dummy variable were used as explanatory variables. The statistical significance of each explanatory variable was tested using the Wald test, and we conducted the same subsequent analyses (likelihood ratio test, AIC comparison, and 95% CI of optima of insect visitation frequency) as described above for the relationship with insect visitation frequency.

All statistical analyses were conducted using R version 4.4.0 (R Core Team, 2024). GLMMs (LMM), ANOVA, AIC model selection, and multiple comparisons were performed using glmmTMB (Brooks et al., 2017), car (Fox & Weisberg, 2019), MuMIn (Bartoń, 2025), and emmeans (Lenth & Piaskowski, 2025) packages, respectively. Application of the Tweedie distribution was conducted with statmod (Giner & Smyth, 2016) and tweedie (Dunn & Smyth, 2008) packages.

RESULTS

Field observations

We observed a total of 1960 insects visiting buckwheat flowers. The buffer radius size of the best models was 200 m according to AIC values (Figure 1E). Insect visitation frequency was positively correlated with forest edge length at this 200-m scale (Figure 1F; Appendix S2: Figure S5, Table S4) and with the estimated volume of floral nectar consumed (Figure 1G; Appendix S2: Table S5A).

A total of 37 bacterial ASV₉₇ belonging to 15 genera were identified (Appendix S2: Figure S3). Taxa commonly found in floral nectar (Quevedo-Caraballo et al., 2025), such as *Pseudomonas*, *Sphingomonas*, *Rosenbergiella*, and *Acinetobacter*, were frequently recorded in our samples (Appendix S2: Figure S3). For bacterial diversity (number of ASV₉₇ per flower and per field), the quadratic term of insect visitation frequency, estimated as significantly negative (Figure 2A,B; Appendix S2: Table S5A), improved the

explanatory power of the model (Appendix S2: Table S5B). Furthermore, the estimated optima of visitation frequency for bacterial diversity existed within the range of observed visitation frequency, based on 95% CI (number of ASV₉₇ per flower = 8.6–10.4, that per field = 9.0–10.7). These results indicate that bacterial diversity had hump-shaped responses to insect visitation frequency at both flower and field scales (Figure 2A,B). Bacterial abundance (log₁₀-transformed CFU per flower and per field) was not significantly correlated with insect visitation frequency (Appendix S2: Figure S6A,B, Table S5), but negatively correlated with the number of ASV₉₇ even when standing nectar volume was taken into consideration (Appendix S2: Figure S7, partial correlation coefficients = −0.35, $t = -2.98$, $df = 64$, $p = 0.004$).

Field experiments

More nectar was consumed by insects in the rough-mesh and no-bag treatments than in the fine-mesh treatment (Figure 1H; Appendix S2: Table S6). Furthermore, nectar consumption was apparent in the rough-mesh and no-bag treatments, but not in the fine-mesh bag treatment (Figure 1H; t test, fine-mesh: $t = 0.08$, $df = 94$, $p = 0.96$; rough-mesh: $t = 7.27$, $df = 94$, $p < 0.001$; no-bag: $t = 8.59$, $df = 94$, $p < 0.001$), which was consistent with the idea that flowers with less exclusive treatment should receive more visitations, although it is possible for bagged flowers to receive a higher number of visitations from smaller insects (e.g., thrips), each of which consumed only a very small amount of nectar.

A total of 58 bacterial ASV₉₇ belonging to 23 genera were identified (Appendix S2: Figure S3), dominated by taxa typical of floral nectar such as *Pseudomonas*, *Sphingomonas*, *Rosenbergiella*, and *Acinetobacter* (Quevedo-Caraballo et al., 2025). Both bacterial diversity (number of ASV₉₇ per flower and per field) and abundance (log₁₀-transformed CFU per flower and per field) differed among the bagging treatments (Figure 2C,D; Appendix S2: Figure S6C,D, Tables S6 and S7). Diversity was higher in the rough-mesh treatment than in the fine-mesh and no-bag treatments (Figure 2C,D; Appendix S2: Tables S6 and S7). Abundance in the fine-mesh bag treatment was higher than in the rough-mesh and no-bag treatments (Appendix S2: Figure S6C,D, Tables S6 and S7). The 95% CI of the optima (number of ASV₉₇ per flower = 2.6–3.7, number of ASV₉₇ per field = 2.9–3.3, CFU per field = 1.7–2.9) was detected within the range of the ordered dummy variable for bagging treatments (except for CFU per flower), suggesting hump-shaped relationships with insect visitation frequency.

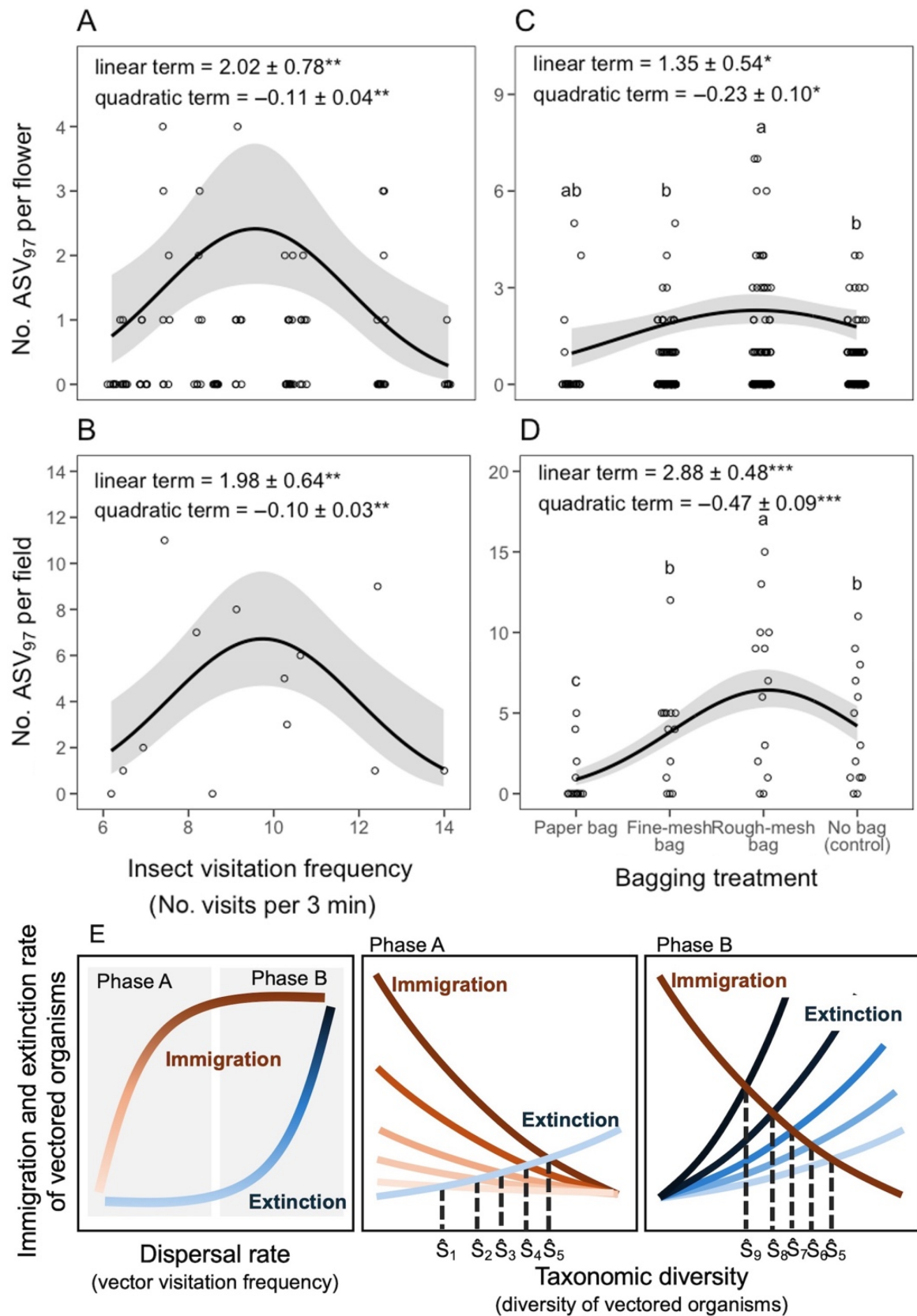


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DISCUSSION

Taken together, two lines of evidence suggest that landscape characteristics affected flower-visiting insects, which then influenced bacterial diversity in nectar (Figures 1E,F, 2A–D). First, insect visitation frequency was likely a good proxy of bacterial dispersal rate, as confirmed by nectar consumption data (Figure 1G,H). Second, a landscape-defined intermediate rate of insect visitation frequency coincided with the highest bacterial diversity observed, a pattern detected at two spatial scales (flower and field) and in both observational and experimental data (Figure 2A–D). As such, our results link microbial diversity in buckwheat flowers, which are roughly 3 mm in radius, to the environmental conditions experienced by their vectoring animals over the comparatively vast scale of 200 m in radius.

Theory suggests that the key mechanism driving the hump-shaped relationship between dispersal rate and species diversity is competitive exclusion (Cadotte, 2006; Mouquet & Loreau, 2003). According to this theory, the number of species in a local habitat patch generally increases as dispersal rate increases, but the probability that dominant competitors colonize in local habitat patches also increases, resulting in competitive exclusion, which leads to a hump-shaped relationship consequently. However, individual buckwheat flowers are short-lived, in bloom for only a single day (Free, 1993), which might be too short for competitive exclusion to play a large role in shaping diversity. So, what might be an additional or alternative explanation for the observed hump-shaped pattern?

One possible explanation concerns the effect of insect visitation on bacterial extinction in addition to immigration. As insects introduce new bacteria to the flower they visit, they also remove some bacteria already present in the nectar through nectar consumption. Thus, insects contribute to both immigration and extinction of microbes in nectar. However, the probability that new bacterial taxa are introduced into a flower probably

increases rapidly at first and then begins to saturate as insect visitation frequency increases further (Loreau & Mouquet, 1999; Mouquet & Loreau, 2003). Meanwhile, when a few insects visit the flower, the probability that all individuals of certain bacterial taxa present in the nectar are removed, that is, a local extinction event, is expected to be low. However, a further increase in insect visitation frequency is likely to increase the probability of extinction exponentially, due to lower bacterial abundance. We note that removal of all nectar may not always result in extinction since some bacteria might potentially survive in residual nectar or on flower surfaces. Still, it seems reasonable to expect that removal of all nectar at least increases the likelihood of extinction. The combined result of this insect-driven immigration and extinction would be a hump-shaped relationship.

One way to conceptualize this hypothesis is to view bacterial diversity as a dynamic balance between immigration and extinction. This model considers two phases with respect to dispersal rate. When dispersal is infrequent (Phase A in Figure 2E), immigration rate, or the rate of new species brought by vectoring insects, increases rapidly with dispersal rate, while extinction rate remains small, resulting in a net increase in diversity. In contrast, when dispersal is frequent (Phase B in Figure 2E), immigration rate saturates as the species pool no longer supplies species that are new to the local community. In the meantime, extinction rate increases exponentially as insects remove more and more bacterial individuals from nectar, causing diversity to decline. These changes in the dynamic balance between immigration and extinction along the dispersal rate axis would result in a hump-shaped relationship between dispersal and diversity.

This model is clearly an oversimplified caricature of reality, but it may still serve as a useful heuristic. The equilibrium assumption made by the model (Figure 2E) is unlikely to be met in real communities of nectar bacteria. However, knowing the equilibrium point to which these communities are attracted can still be informative

FIGURE 2 Empirical evidence and conceptual model on dispersal–diversity relationships. Results of field observations (A, B) and experiments (C, D) show the estimated relationship of bacterial diversity with insect visitation frequency (A, B) and the effects of bagging treatment (Figure 1D) on bacterial diversity (C, D). For the number of ASV₉₇ per flower (A, C), each dot represents each of all nectar samples. To deal with zero inflation in the data set, regression lines were estimated using the top 30% data points in each of 10 bins that were equally divided in the range of insect visitation frequency, or in each of the bagging treatments (see the statistical analyses section). The shaded range of estimates indicates the 95% CI. Different letters indicate significant difference ($p < 0.05$). *: $p < 0.05$, **: $p < 0.01$, ***: $p < 0.001$. Detailed statistics are shown in Appendix S2: Tables S5–S7. (E) Hypothesized relationship between insect visitation frequency, the rate of immigration and extinction in nectar bacteria in flowers, and the taxonomic diversity of nectar bacteria per flower or per field. The symbol $\hat{S}_n$ denotes the predicted equilibrium level of taxonomic diversity, numbered from 1 to 9 in order of insect visitation frequency. This conceptual model predicts a hump-shaped relationship between insect visitation frequency and bacterial taxonomic diversity. Darker hues of the lines indicate the higher rate of immigration and extinction.

in understanding diversity patterns, even when communities are in a nonequilibrium state (Fukami & Nakajima, 2011; Roughgarden, 1998). Similarly, simple models like this should be treated with caution because they ignore other factors that may also affect diversity. For example, nectar consumption by insects may affect bacterial population size not just directly by removal from nectar, but also indirectly by altered temperature or oxygen availability in nectar. Furthermore, regardless of nectar consumption, some plants may alter their nectar secretion and antimicrobial compounds in response to pollination and microbial colonization (Schmitt et al., 2021; Stpiczyńska, 2003), potentially influencing bacterial growth and persistence. The model may be best used as a conceptual foundation on which to add these additional factors.

Hump-shaped patterns were observed in both diversity (Figure 2A–D) and abundance (see also Appendix S1: Section S4; Appendix S2: Figure S6C,D), which would not be necessarily expected only by the theory of competitive exclusion. We would expect only diversity to decline under high insect visitation frequency, without a significant change in abundance, if competitive exclusion was the cause of the diversity decline with increased visitation frequency. For example, the Lotka–Volterra interspecific competition model predicts that the dominant competitor will be more abundant as a result of competitive exclusion, compensating for reduction in the abundance of competitively inferior species. On the other hand, we would expect hump-shaped patterns in both diversity and abundance if increased extinction accompanied increased immigration.

Given the results we present here, we suggest that future research can strengthen the rigor and scope of the inferences drawn in this study in three ways. First, it has become clear through this study that quantifying both immigration and extinction, not just immigration, is important in understanding how vector-mediated dispersal affects diversity. We found no clear difference in bacterial taxonomic composition among the bagging treatments (Appendix S2: Figures S2 and S3), suggesting no clear differences among bacterial taxa in their tendency to immigrate or go extinct and among insects in their vectoring bacterial taxa. However, it would be informative to more directly study which bacteria insects tend to bring to nectar and which they tend to remove from nectar. This work could involve examining bacteria in the mouthparts of flower-visiting insects (Warren et al., 2025) before and after flower visits.

Second, this study quantified insect visitation frequency rather coarsely by looking at overall frequency without considering the taxonomic identity of the insects. Studying the contribution of different insects to microbial

dispersal in more detail could reveal more nuanced relationships between dispersal and diversity than were possible in this study. Experimental exclusion of specific insect groups would help for this purpose. Exclusion is feasible with ants, for example, which are major pollinators of buckwheat (Natsume et al., 2022).

Finally, this study did not consider the variation among insect species in their foraging distance, which can be substantial, with smaller arthropods such as ants and thrips moving over just a few meters or less per day (Rhainds & Shipp, 2004), while bees, beetles, butterflies, and other winged insects move across several hundred meters or more on a daily basis (e.g., Danforth et al., 2019). These insects are likely to contribute to microbial dispersal among flowers at greatly different scales. Short-distance movement contributes to internal dispersal (i.e., dispersal of species across local communities within a metacommunity, *à la* Leibold et al., 2004). In our case, this scale may correspond to dispersal within a buckwheat field. In contrast, long-distance movement contributes to external dispersal (i.e., supply of species to local communities from the regional species pool, unaffected by the population dynamics happening within metacommunities, *à la* MacArthur & Wilson, 1967). Theoretical work suggests that internal and external dispersal can interactively influence diversity (Fukami, 2005). Future studies that examine how different insect groups contribute to microbial dispersal at various spatial scales could provide a deeper understanding of vector-mediated dispersal. Although limited in scope, a preliminary analysis of the data we present in this paper suggests that small and large insects, likely contributing more to internal and external dispersal, respectively, determine bacterial diversity in a highly interactive manner (Appendix S2: Figure S8).

In conclusion, we have shown here that landscape context can indirectly shape diversity patterns in vector-dispersed organisms by affecting the vectors. This finding led us to consider the possibility that the intermediate dispersal pattern may be common in vector-dispersed organisms even when competitive exclusion does not play a large role. This hypothesis (Figure 2E) seems possible whenever the vectored organisms and/or their habitat patches are consumable resources for their dispersal vectors, a scenario widely observed in a range of phoretic organisms. Besides nectar microbes, other potential examples include fruit-inhabiting microbes dispersed by frugivorous insects, carrion-inhabiting microbes dispersed by scavenging insects, and herbaceous plants dispersed by herbivorous mammals, among others (Bartlow & Agosta, 2021). Although less studied than vector-independent dispersal, vector-mediated dispersal is a common phenomenon across many taxa (e.g., Borgmann-Winter et al., 2023;

Lovas-Kiss et al., 2020; Plue & Cousins, 2018; Soons et al., 2016; Suetsugu et al., 2018). More research on vector-mediated dispersal should help to develop a deeper understanding of how dispersal affects biodiversity.

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CONFLICT OF INTEREST STATEMENT

The authors declare no conflicts of interest.

DATA AVAILABILITY STATEMENT

Data and code (Nagano, 2025) are available in Figshare at <https://doi.org/10.6084/m9.figshare.30423895.v3>.

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SUPPORTING INFORMATION

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