Joint species distribution modelling of insect microbiota: Time to jump onto a new opportunity

Ovaskainen, Otso[1], Łukasik, Piotr[2] and Roslin, Tomas[3,4]

[1]Department of Biological and Environmental Science, University of Jyväskylä, P.O. Box 35, 40014 Jyväskylä, Finland

[2]Institute of Environmental Sciences, Faculty of Biology, Jagiellonian University, Kraków, Poland

[3]Ecosystems and Environment Research Programme, Faculty of Biological and Environmental Sciences, University of Helsinki, Helsinki, Finland

[4]Department of Ecology, Swedish University of Agricultural Sciences (SLU), Uppsala, Sweden

Corresponding author: Otso Ovaskainen. Email otso.t.ovaskainen@jyu.fi

Abstract

How microbes influence insects, each other and *vice versa*, is a topical question in insect science. With this contribution, we highlight joint species distribution models (JSDMs) as a statistical framework particularly well suited for resolving it. While JSDM has been widely applied to microbiota of organisms other than insects, only a handful of studies have applied them thus far to insect microbiota. To encourage insect microbiota researchers to catch up with the benefits of JSDM, we introduce the statistical and ecological basics of JSDM and give flesh to the modelling framework by reviewing how it has so far been applied to insect microbiota. We highlight the power of JSDMs in separating host, environmental and microbial drivers of community assembly, and in generating hypotheses about how different microbes influence each other. To stimulate a broad adoption of JSDMs in studies of insect microbiota, we propose a predictive framework for identifying and characterizing five ecological categories of insect-associated microbes: (1) obligate nutritional symbionts; (2) facultative endosymbionts; (3) specialized gut associates; (4) transient microbes; and (5) pathogens and parasites. In particular, we hypothesize how the ecological characteristics of these different microbial categories are reflected in the statistical signatures recovered by JSDMs. We further suggest how JSDM can be applied to address the phylogenetic and ecological scales at which microbiome patterns are structured and to uncover how global environmental changes may reshape insect microbiota.

Keywords: insect microbiome, Joint Species Distribution Modelling (JSDM), Hierarchical Modelling of Species Communities (HMSC), host-microbe associations, symbiosis, community assembly, species interactions

Highlights:

- Different kinds of insect-associated microbes generate different JSDM signatures
- JSDM can separate host, environmental and microbial drivers of community assembly
- JSDM remains little used for insect microbiota, but is much used for other microbiotas
- JSDM can move insect microbiome research from description to ecological inference

Introduction

Microbes can fundamentally alter the dynamics of insect populations and communities—and insects, on their part, serve as both hosts and vectors of microbes (1,2). Reflecting the growing insight into the importance of insect–microbe interactions, research on insect microbiota has rapidly increased over the past decade (Fig. 1, green line). At the same time, research developing or applying joint species distribution modelling (JSDM) has increased at much the same rate (Fig. 1, black line). Importantly, many of the ecological questions gaining attention in current insect microbiome research are resolvable by JSDM (3). Microbiome studies frequently ask how host species, host populations, environmental conditions, and interactions among microbes shape microbial community composition. As such processes often act simultaneously, it remains difficult to distinguish their relative importance using conventional analytical approaches. JSDM has been explicitly designed to resolve the relative contributions of multiple drivers spanning several levels of biological organization. JSDM can be especially powerful in disentangling the processes structuring microbial co-occurrence networks: which microbes are found together because of shared niche (e.g. host or environmental conditions), and which are found together because they facilitate each other (3,4).

Despite the apparent match between the analytical challenges of insect microbiota studies and the strengths of JSDM, only a handful of studies have thus far applied JSDM for insect microbiota (Fig. 1, red line). Instead, JSDM has been widely applied to microbiota of organisms other than insects (Fig. 1, brown line), including humans (5), primates other than humans (6), mammals other than primates (7), birds (3), fishes (8), amphibians (9), sponges (3), ticks (10) and plants (11), as well as to microbiota inhabiting soil (12) and dead wood (13).

That JSDM remain underused in studies of insect microbiota appears a missed opportunity. The main purpose of this article is to encourage insect microbiota researchers to catch up with the benefits of JSDM and thus to start making full use of this powerful tool. We first recapitulate the statistical and ecological basics of JSDM, then give flesh to the modelling framework by reviewing how it has so far been applied to studies of insect microbiota, and finally discuss how JSDM could provide a systematic framework for understanding—and predicting—how different types of insect-microbe associations are structured, maintained and affected by global change.

What is joint species distribution modelling?

Single species distribution models (SDMs) are widely applied statistical tools for analysing how the occurrences or abundances of a focal species depend on variation in the abiotic and biotic environmental conditions, as well as on other factor that vary in space and time (14). As an example of insect-microbiota studies, (15) used generalized linear mixed modelling (GLLM) to test how the prevalence of a bacterial symbiont *Wolbachia* varies across space and time in a grasshopper species. As the simplest extension of SDMs to the many-microbes case, stacked species distribution modelling fits a SDM *independently* for each microbe, and then makes inferences or predictions based on such as a collection of models (16).

In contrast, with joint species distribution models (JSDM), the model parameters are estimated *jointly* for all microbes (4,17,18). JSDMs are hence multivariate models where the response

variable is a vector, e.g., the presences of all microbial symbionts within a host individual (Box 1). Fitting the model simultaneously to many microbes brings two distinct advantages. First, JSDM allows us to estimate how microbes' dependency on their hosts and environments depend on their phylogenetic relationships, thus relating niche variation to shared evolutionary history (4,19). Second, JSDMs estimate residual associations among microbes that remain unexplained after accounting for host- and environmental factors (4). Thus, as compared to the identification of microbial co-occurrences directly from the raw data, residual associations identified by JSDM can bring additional resolution for identifying both positive and antagonistic interactions among different microbes – for example, protection conferred by a mutualistic bacterium against a pathogen. We argue that this flexibility of JSDMs makes them particularly well suited to insect microbiota, whose members differ fundamentally in transmission modes, host specificity and ecological function (1,20). Furthermore, JSDMs have recently greatly improved in their computational scalability, enabling their application to thousands (21) or even hundreds of thousands (22) of microbial taxa.

What have JSDMs revealed about insect-associated microbes?

To date, only four papers have explicitly applied JSDM to insect microbiota (for our literature search, see Fig. 1). While all four applied the HMSC framework (4), they addressed markedly different biological systems and questions (Table 1). In terms of the host community considered, (23) focused on a single butterfly species, (24) on bacterial and fungal microbiota of two mosquito species, (25) on pathogens in diverse bumblebees and (26) on bacterial communities associated with species-rich assemblages of phorid flies (Table 1). Likewise, the studies differed in their analytical approaches, with (25) analysing PCR-based presence-absence data for viruses and other pathogens, while the three other studies used marker gene amplicon sequencing to characterizing bacterial (and in case of (24) also fungal) communities (Table 1).

Variation in the types of the host and microbiome communities was reflected in the questions addressed by the four studies and hence in the fixed and random effects included in their JSDMs (Table 1). All studies, except the single-species study of (23), asked how the microbiota variation was structured by the host species. (24) included the contrast between the two hosts as a fixed effect, whereas (25) and (26) treated their diverse sets of host species as random effects (Table 1). (26) and (24) further quantified within-species host genetic variation using COI haplotypes, and all studies except (25) considered the effect of the sex of the host individual. Importantly, and as something that the JSDM approach specifically supports, all four studies included the host individual as a community-level random effect, allowing variation among individual hosts to be quantified after accounting for the host and environmental factors measured. In addition to these host-related predictors, the studies controlled for environmental variation that they expected to influence host microbiota, as well as factors implied by their study designs—such as the random effect of the sampling site (Table 1). The studies based on high-throughput sequencing accounted for the zero-inflated nature of the data through a hurdle-approach, i.e. separate modelling of microbial presence and then abundance-when-present, while the PCR-detection based study of (25) restricted their analyses to presence-absence data.

These four studies illustrate the ability of JSDMs to partition microbiome variation among host-, environmental- and individual-level components, while simultaneously generating hypotheses about microbial associations. The pathogen-focused study by (25) found the host species to be the

dominant source of variation, suggesting a high degree of host specificity among the pathogens considered. In contrast, a consistent finding from all three studies on bacterial and fungal microbiomes was that host species, host genotype and host sex explained only a minor proportion of variation in the overall microbial community composition, despite some individual microbial taxa exhibiting strong responses. Instead, all three studies identified host individual as the dominant source of microbial variation, highlighting substantial heterogeneity among individual insects beyond that captured by the host and environmental variables measured. The residual associations estimated by the models differed among studies, reflecting differences in the ecological structure of the microbial communities investigated. (23) found a strong negative association between Enterobacteriaceae and bacteria belonging to other families, suggesting competitive exclusion among bacterial clades. In contrast, (24) and (26) reported predominantly positive associations among microbial taxa, suggesting a nested community structure. While these associations are likely to reflect ecological interactions among the microbes, they may also reflect the influences of some unmeasured host-specific factors. This uncertainty remains because these two explanations cannot be conclusively disentangled from each other without additional data from manipulative experiments (4,27).

While the four studies reviewed above appear to be the only explicit applications of JSDMs to insect microbiota, other studies have used related approaches. As one example, (28) used HMSC to examine how treatment by *Bacillus thuringiensis* var. *israelensis* (a naturally occurring soil bacterium used as a biological larvicide) influenced chironomid communities—effectively reversing the perspective adopted by the other studies, by modelling insects as the response community. As a second example, (29) modelled vector–virus–microbiome interactions, asking how a microbial symbiont of an aphid influenced the probability of virus acquisition. As they considered just one microbe and just one virus, instead of the more generic JSDM they applied a system-tailored hierarchical model connecting microbe, virus and environmental conditions. As a third example, (30) investigated the distribution of viruses across 13 species of bumblebees. Similarly to what could be achieved with JSDM, they examined factors influencing individual-level probabilities of infection but used a co-phylogenetic model to focus specifically on the interplay between the host and the virus phylogenies. This approach revealed that while the interaction between the hosts and the viruses were generally unpredictable, closely related species were more likely to exhibit similar patterns of infection.

How could JSDM help advancing research in insect microbiota?

We propose that systematic application of JSDM approaches can play a major role in addressing three core questions related to insect microbiota:

How to identify and characterize major ecological categories of insect-associated microbes? The four studies summarized in Table 1 highlight how the ecological characteristics of microbial communities are reflected in the statistical signatures recovered by JSDMs. These studies span three broad ecological categories of insect-associated microbes: transient microbial communities (23,24), facultative endosymbionts embedded within diverse and largely transient bacterial communities (26), and pathogens (25). Building on this evidence and ecological reasoning, we foresee a more general use of JSDM outputs for identifying major ecological categories of insect-associated microbes (Table 2). Applying JSDMs across diverse insect species and populations will allow

the predictions of Table 2 to be tested for microbes whose roles have already been revealed, as well as hypothesizing ecological roles of newly discovered microbes whose biology remains uncertain. The power of JSDMs for doing so relates to their ability to quantify the relative contributions of different types of host-specific and environmental factors that may favour particular symbionts or shape symbiont-mediated host responses (26). JSDM analyses can further facilitate the distinction between stable, vertically transmitted obligate symbionts and facultative symbionts including reproductive manipulators or defensive mutualists, pathogens, and environmentally acquired associates.

At what phylogenetic and ecological scales are microbiome patterns structured? Microbiome variation can be analyzed at multiple levels of biological resolution, ranging from bacterial genera to ASVs and from host populations to higher insect clades (31,32). Comparing JSDMs fitted across these scales can distinguish long-term evolutionary associations from recent ecological processes, revealing the biological scales at which microbiome assembly is most predictable and identifying which patterns are evolutionarily conserved versus environmentally contingent.

How does global environmental change reshape insect microbiota? Heat stress, pesticides, habitat modification, introduced species and other anthropogenic disturbances alter insect communities and, undoubtedly, their microbiota, yet the mechanisms underlying these effects remain poorly understood (1,33,34). By simultaneously modelling host-, environment- and microbe-associated drivers of community composition, JSDM provides a framework for identifying how environmental change propagates through insect-associated microbial communities, and how microbial symbionts buffer insect hosts against environmental stress or alternatively amplify the consequences of environmental change.

In conclusion, we consider that systematic application of JSDMs can move insect microbiome research beyond describing community composition towards testing general ecological and evolutionary hypotheses.

Acknowledgments

OO was funded by the Research Council of Finland (RCF, grants no. 336212 and 345110), TR by RCF (grant no. 376888) and by the Swedish Research Council *Vetenskapsrådet* (grant no. 2023-05118), and PŁ by the Polish National Science Centre (grants no. 2018/31/B/NZ8/01158 and 2021/43/B/NZ8/03376).

Declaration of interest: none.

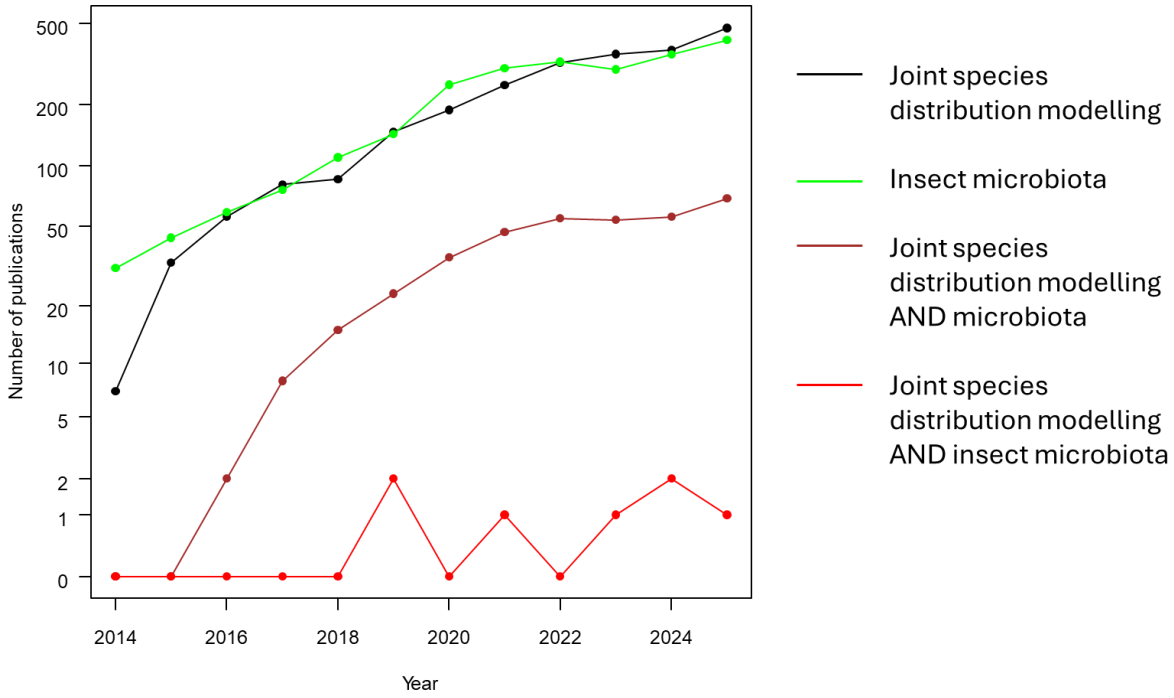
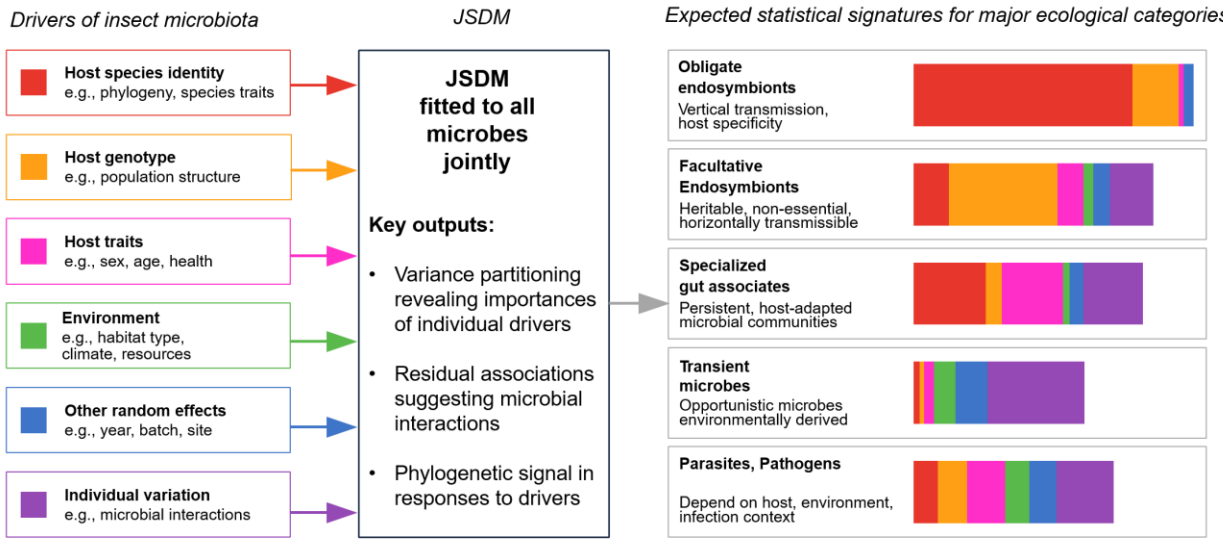


Figure 1. Joint species distribution modelling remains little utilized in studies of insect microbiota. The figure shows yearly numbers of publications in the Dimensions scientific research database (app.dimensions.ai; accessed June 8th 2026) as identified by the search terms (1) "Joint species distribution modelling", (2) "Insect microbiota", (3) "Joint species distribution modelling" and "microbiota", or (4) "Joint species distribution modelling" and "insect microbiota". For "modelling", also "modeling" or "model" were accepted, and for "microbiota", also "microbiome" was accepted. Note the logarithmic scaling of the y-axis.

Box 1. JSDM as statistical framework for studying insect microbiota.



The figure illustrates how drivers of microbiota composition enter as JSDM input, and how JSDM outputs are expected to reflect ecological characteristics of the studied communities. Like single species distribution models, JSDM approaches can be built within many kinds of statistical frameworks (4,46,47). Among the most popular approaches are generalized linear latent variable models (18,48,49), which directly generalize GLLMs for multiple species. We exemplify here the statistical structure of JSDM through Hierarchical Modelling of species communities (HMSC) (4,50). In HMSC notation, the species data are denoted by y_{ij}, where i indexes the sampling units and j the species. The underlying linear predictor is modelled as a function of fixed effects and latent variables: $L_{ij} = \Sigma_k x_{ik}\beta_{kj} + \Sigma_h \eta_{ih}\lambda_{hj}$. Concerning the fixed effects, x_{ik} is the value of the predictor k in sampling unit i, and β_{kj} is the response of species j to this predictor. Variation among the species responses β_{kj} can be captured by a second-level regression model that uses species traits as predictors and phylogenetic relationships as the variance-covariance structure (19,50). Concerning the latent variables, η_{ih} represents some latent (unknown or unmeasured) environmental (or other) conditions of the sampling unit i, whereas the term λ_{hj} measures how the species respond to that latent variable. While for the fixed effects the environmental conditions (x_{ik}) have been measured and only the species responses to them (β_{kj}) are estimated, for the latent variable part of the model both the latent variables (η_{ih}) and the species responses to them (λ_{hj}) are estimated. Co-occurrence patterns among the species can then be quantified by the species-to-species variance-covariance matrix $\mathbf{\Omega}$, with element $\Omega_{j_1 j_2} = \Sigma_h \lambda_{hj_1}\lambda_{hj_2}$ measuring the level of co-occurrence between species j_1 and j_2 (4).

Table 1. Key characteristics of the four studies that have applied joint species distribution modelling to insect microbiota.

Reference	(23)	(24)	(25)	(26)
Host community	One butterfly species (*Melitaea cinxia*).	Two mosquito species (*Ochlerotatus impiger* and *O. nigripes*).	22 species of bumblebees.	75 species of scuttle flies (Diptera: Phoridae).
Microbial community	Bacterial (16S rRNA V5-V6 region) OTUs (n=562) detected with high-throughput sequencing (HTS).	Bacterial (16S rRNA V4 region) OTUs (n=418) and fungal (ITS2) OTUs (n=51) detected with HTS.	Viruses (n=5) and other pathogens (n=4) detected with PCR methods.	Bacterial communities represented either by 16S rRNA V4 region OTUs (n=50), 16S-V4 ZOTUs (n=100), or *Wolbachia* COI ZOTUs (n=24) detected with HTS.
Fixed effects	The sex and infection status of the host individual. The abundance of the focal OTU, the OTU community composition, and the metabolite composition of the host plant.	The interaction between host species and the sex of the host individual. Sequencing depth.	Altitude, annual mean temperature and annual precipitation of the sampling locality.	The sex of the host individual and the season of sampling.
Random effects implemented through latent variables.	The host plant (n=55) and the host individual (n=142).	The sampling site (n=5), the year of collection (n=5), the COI haplotype of the host (n=40), and the host individual (n=400 for bacteria and 364 for fungi)	The sampling site (n=19), the host species (n=22) and the host individual (n=771).	The sampling site (n=6), the host species (n=75), the host genotype (n=328) and the host individual (n=1634).
Model type	Hurdle approach: probit model for presence–absence, lognormal model for abundance conditional on presence.	Hurdle approach: probit model for presence–absence, lognormal model for abundance conditional on presence.	Probit model for presence–absence.	Hurdle approach: probit model for presence–absence, lognormal model for abundance conditional on presence.

Table 2. Predicted statistical signatures of major functional categories of insect-associated microbes in joint species distribution models. The symbols denote the expected relative importance of each component (***high,**moderate, *low). The predictions are derived from the following considerations: *Obligate nutritional symbionts*, such as *Buchnera* in aphids (35), are expected to show extremely strong host specificity, with little contribution from environmental factors or variation among individuals (36). More recently acquired heritable symbionts may exhibit similar patterns, although these may be obscured by rapid sequence evolution and frequent gains or losses within host lineages (37). *Facultative endosymbionts*, such as *Wolbachia*, are vertically transmitted yet occasionally switch hosts, allowing both host-related and environmental factors to shape their distributions (38). Simultaneously, they can interact with other members of the microbiota (39,40). *Specialized gut associates,* such as those of honeybees, often show remarkably stable composition, yet their abundances vary substantially with host age, diet, health, season, parasite and pathogen load and environmental stress (41,42). Diverse *transient microbes* opportunistically colonize different environments (including insect bodies), and their occurrence may depend primarily on environmental exposure and vary strongly among environments and individuals (43). *Pathogens and parasites* of insects, as well as pathogens vectored by insects, often exhibit strong host specificity but are also influenced by geography, seasonality, and co-occurrence with other microbes (44,45).

Functional category	**Example**	**Prevalence**	**Transmission**	**Host specificity**	**Expected variance partitioning**					**Microbial associations**
					Species	Genotype	Population	Environment	Individual	
Obligate nutritional symbionts	*Buchnera* (aphids)	~100%	Strictly vertical	Very high	***	*				Rare
Facultative endosymbionts	*Wolbachia*, *Spiroplasma*	Intermediate, variable	Vertical, occasional host switches	Medium to high	*	***	***	*	***	Strong positive & negative interactions
Specialized gut associates	*Snodgrassella*, *Gilliamella* (honeybees)	Very high	Social, maternal, environmental	High	**	**			*	Structured co-occurrence
Transient microbes	*Pseudomonas*, *Enterobacter*	Low	Environmental	Low			*	**	***	Inconsistent
Pathogens and parasites	*Nosema, Crithidia* (bees), *Phytoplasma*	Variable	Horizontal, vector-mediated	Variable	**	*	**		***	Co-infection and exclusion networks

References and recommended reading

Papers of particular interest, published within the period of review, have been highlighted as:
* of special interest
** of outstanding interest

1.* Łukasik P, Kolasa MR. With a little help from my friends: the roles of microbial symbionts in insect populations and communities. Phil Trans Roy Soc B. 2024 Jun 24;379(1904). doi:10.1098/rstb.2023.0122

Reviews the ecological diversity of insect-associated microbes, providing the biological framework underlying the functional categories discussed in this review.

2. Douglas AE. Insects and Their Beneficial Microbes. Princeton University Press; 2022.
3. Björk JR, Hui FKC, O'Hara RB, Montoya JM. Uncovering the drivers of host-associated microbiota with joint species distribution modelling. Mol Ecol. 2018 Jun 4;27(12):2714–24. doi:10.1111/mec.14718
4. Ovaskainen O, Abrego N. Joint species distribution modelling. Cambridge University Press; 2020. doi:10.1017/9781108591720
5. Wang Z, Jenabian MA, Alexandrova Y, Pagliuzza A, Olivenstein R, Samarani S, et al. Interplay between the Lung Microbiome, Pulmonary Immunity and Viral Reservoirs in People Living with HIV under Antiretroviral Therapy. Viruses. 2022 Oct 29;14(11):2395. doi:10.3390/v14112395
6. Aivelo T, Norberg A. Parasite–microbiota interactions potentially affect intestinal communities in wild mammals. Journal of Animal Ecology. 2018 Mar 3;87(2):438–47. doi:10.1111/1365-2656.12708
7. Lin D, Lacey EA, Bach BH, Bi K, Conroy CJ, Suvorov A, et al. Gut microbial diversity across a contact zone for California voles: Implications for lineage divergence of hosts and mitonuclear mismatch in the assembly of the mammalian gut microbiome. Mol Ecol. 2020 May 15;29(10):1873–89. doi:10.1111/mec.15443
8. Nyholm L, Odriozola I, Martin Bideguren G, Aizpurua O, Alberdi A. Gut microbiota differences between paired intestinal wall and digesta samples in three small species of fish. PeerJ. 2022 Feb 22;10:e12992. doi:10.7717/peerj.12992
9. Medina D, Martins RA, Prist PR, Buttimer S, Neely WJ, Schuck LK, et al. Connecting habitats, boosting disease resistance: Spatial connectivity enhances amphibian microbiome defenses against fungal pathogen. Proceedings of the National Academy of Sciences. 2026 Apr 28;123(17). doi:10.1073/pnas.2520745123
10. Aivelo T, Norberg A, Tschirren B. Bacterial microbiota composition of *Ixodes ricinus* ticks: the role of environmental variation, tick characteristics and microbial interactions. PeerJ. 2019 Dec 19;7:e8217. doi:10.7717/peerj.8217
11. Sallinen S, Norberg A, Susi H, Laine AL. Intraspecific host variation plays a key role in virus community assembly. Nat Commun. 2020 Nov 5;11(1):5610. doi:10.1038/s41467-020-19273-z
12. Lammel DR, Barth G, Ovaskainen O, Cruz LM, Zanatta JA, Ryo M, et al. Direct and indirect effects of a pH gradient bring insights into the mechanisms driving prokaryotic community structures. Microbiome. 2018 Dec 11;6(1):106. doi:10.1186/s40168-018-0482-8

13. Saine S, Fukami T, Penttilä R, Furneaux B, Ovaskainen O, Abrego N. Experimental species introductions influence fungal community succession through positive and negative effects on resident species. ISME Communications. 2025 Jan 17;5(1). doi:10.1093/ismeco/ycaf166
14. Guisan A, Thuiller W, Zimmermann NE. Habitat Suitability and Distribution Models. Cambridge University Press; 2017. doi:10.1017/9781139028271
15. Martínez-Rodríguez P, Rolán-Alvarez E, del Mar Pérez-Ruiz M, Arroyo-Yebras F, Carpena-Catoira C, Carvajal-Rodríguez A, et al. Geographic and Temporal Variation of Distinct Intracellular Endosymbiont Strains of Wolbachia sp. in the Grasshopper Chorthippus parallelus: a Frequency-Dependent Mechanism? Microb Ecol. 2019 May 14;77(4):1036–47. doi:10.1007/s00248-019-01338-2
16. Calabrese JM, Certain G, Kraan C, Dormann CF. Stacking species distribution models and adjusting bias by linking them to macroecological models. Global Ecology and Biogeography. 2014 Jan 11;23(1):99–112. doi:10.1111/geb.12102
17. Pollock LJ, Tingley R, Morris WK, Golding N, O'Hara RB, Parris KM, et al. Understanding co-occurrence by modelling species simultaneously with a Joint Species Distribution Model (JSDM). Methods Ecol Evol. 2014 May 19;5(5):397–406. doi:10.1111/2041-210X.12180
18. Warton DI, Blanchet FG, O'Hara RB, Ovaskainen O, Taskinen S, Walker SC, et al. So many variables: joint modeling in community ecology. Trends Ecol Evol. 2015 Dec;30(12):766–79. doi:10.1016/j.tree.2015.09.007
19. Abrego N, Norberg A, Ovaskainen O. Measuring and predicting the influence of traits on the assembly processes of wood-inhabiting fungi. Journal of Ecology. 2017 Jul 6;105(4):1070–81. doi:10.1111/1365-2745.12722
20. Perreau J, Moran NA. Genetic innovations in animal–microbe symbioses. Nat Rev Genet. 2022 Jan 13;23(1):23–39. doi:10.1038/s41576-021-00395-z
21. Rahman AU, Tikhonov G, Oksanen J, Rossi T, Ovaskainen O. Accelerating joint species distribution modeling with Hmsc-HPC: A 1000x faster GPU deployment. PLoS Comp Biol. 2024;20:e1011914.
22.* Ovaskainen O, Winter S, Tikhonov G, Abrego N, Anslan S, deWaard JR, et al. Common to rare transfer learning (CORAL) enables inference and prediction for a quarter million rare Malagasy arthropods. Nat Methods. 2025 Oct 23;22(10):2074–82. doi:10.1038/s41592-025-02823-y

Demonstrates how JSDM can be extended to hundreds of thousands of species, and how rare species can be included in community-level inference.

23. Minard G, Tikhonov G, Ovaskainen O, Saastamoinen M. The microbiome of the *Melitaea cinxia* butterfly shows marked variation but is only little explained by the traits of the butterfly or its host plant. Environ Microbiol. 2019 Nov 9;21(11):4253–69. doi:10.1111/1462-2920.14786
24. Rojas-Guerrero D, Kolasa M, Buczek M, Prus-Frankowska M, Nowak KH, Roslin T, et al. Cold and lonely: low-abundance microbiota and no core microbiome across a broad geographic sampling of a mosquito species in Greenland. bioRxiv [Internet]. 2024 Aug 28;10.1101/2024.08.27.609970. Available from: http://biorxiv.org/lookup/doi/10.1101/2024.08.27.609970

25. Chen H, Zhang G, Ding G, Huang J, Zhang H, Vidal MC, et al. Interspecific Host Variation and Biotic Interactions Drive Pathogen Community Assembly in Chinese Bumblebees. Insects. 2023 Nov 17;14(11):887. doi:10.3390/insects14110887
26.** Nowak KH, Hartop E, Prus-Frankowska M, Buczek M, Kolasa MR, Roslin T, et al. What lurks in the dark? An innovative framework for studying diverse wild insect microbiota. Microbiome. 2025 Aug 12;13(1):186. doi:10.1186/s40168-025-02169-9

Applies JSDM to a diverse insect community and demonstrates that different microbial functional groups exhibit distinct statistical signatures, highlighting the power of JSDMs for ecological inference.

27. Blanchet FG, Cazelles K, Gravel D. Co-occurrence is not evidence of ecological interactions. Ecol Lett. 2020 Jul 19;23(7):1050–63. doi:10.1111/ele.13525
28.* Röder N, Stoll VS, Jupke JF, Kolbenschlag S, Bundschuh M, Theißinger K, et al. How non-target chironomid communities respond to mosquito control: Integrating DNA metabarcoding and joint species distribution modelling. Science of The Total Environment. 2024 Feb;913:169735. doi:10.1016/j.scitotenv.2023.169735

Illustrates the versatility of JSDM by reversing the perspective and modelling insect community responses to microbial biocontrol, highlighting their broad applicability beyond host–associated microbiota.

29. Enders L, Hefley T. Modeling host–microbiome interactions to improve mechanistic understanding of aphid vectored plant pathogens. Front Ecol Evol. 2023 Sep 27;11. doi:10.3389/fevo.2023.1251165
30. Pascall DJ, Tinsley MC, Obbard DJ, Wilfert L. Host evolutionary history predicts virus prevalence across bumblebee species [Internet]. 2018. Available from: http://biorxiv.org/lookup/doi/10.1101/498717 doi:10.1101/498717
31. Brooks AW, Kohl KD, Brucker RM, van Opstal EJ, Bordenstein SR. Phylosymbiosis: Relationships and Functional Effects of Microbial Communities across Host Evolutionary History. PLoS Biol. 2016 Nov 18;14(11):e2000225. doi:10.1371/journal.pbio.2000225
32. Sanders JG, Powell S, Kronauer DJC, Vasconcelos HL, Frederickson ME, Pierce NE. Stability and phylogenetic correlation in gut microbiota: lessons from ants and apes. Mol Ecol. 2014 Mar 6;23(6):1268–83. doi:10.1111/mec.12611
33. Wagner DL, Grames EM, Forister ML, Berenbaum MR, Stopak D. Insect decline in the Anthropocene: Death by a thousand cuts. PNAS. 2021 Jan 12;118(2):e2023989118. doi:10.1073/pnas.2023989118
34.* Graber LC, Moreau CS. Insect–microbiome interactions in a changing world. Curr Opin Insect Sci. 2026 Jun;75:101495. doi:10.1016/j.cois.2026.101495

Reviews how global environmental change reshapes insect microbiota, identifying emerging questions ideally suited for JSDM-based ecological inference.

35. Norberg A, Abrego N, Blanchet FG, Adler FR, Anderson BJ, Anttila J, et al. A comprehensive evaluation of predictive performance of 33 species distribution models at species and community levels. Ecol Monogr. 2019 Aug 12;89(3). doi:10.1002/ecm.1370

36. Wilkinson DP, Golding N, Guillera-Arroita G, Tingley R, McCarthy MA. A comparison of joint species distribution models for presence–absence data. Methods Ecol Evol. 2019 Feb 3;10(2):198–211. doi:10.1111/2041-210X.13106
37. Niku J, Hui FKC, Taskinen S, Warton DI. gllvm: Fast analysis of multivariate abundance data with generalized linear latent variable models in R. Methods Ecol Evol. 2019 Dec 22;10(12):2173–82. doi:10.1111/2041-210X.13303
38. Ovaskainen O, Abrego N, Halme P, Dunson D. Using latent variable models to identify large networks of species-to-species associations at different spatial scales. Methods Ecol Evol. 2016 May 18;7(5):549–55. doi:10.1111/2041-210X.12501
39. Ovaskainen O, Tikhonov G, Norberg A, Guillaume Blanchet F, Duan L, Dunson D, et al. How to make more out of community data? A conceptual framework and its implementation as models and software. Ecol Lett. 2017 May 20;20(5):561–76. doi:10.1111/ele.12757
40. Chong RA, Park H, Moran NA. Genome evolution of the obligate endosymbiont Buchnera aphidicola. Mol Biol Evol. 2019 Jul 1;36(7):1481–9. doi:10.1093/molbev/msz082
41. Moran NA, McCutcheon JP, Nakabachi A. Genomics and evolution of heritable bacterial symbionts. Annu Rev Genet. 2008 Dec 1;42(1):165–90. doi:10.1146/annurev.genet.41.110306.130119
42. McCutcheon JP, Boyd BM, Dale C. The life of an insect endosymbiont from the cradle to the grave. Curr Biol. 2019 Jun;29(11):R485–95. doi:10.1016/j.cub.2019.03.032
43. Kaur R, Shropshire JD, Cross KL, Leigh B, Mansueto AJ, Stewart V, et al. Living in the endosymbiotic world of Wolbachia: A centennial review. Cell Host Microbe. 2021 Jun;29(6):879–93. doi:10.1016/j.chom.2021.03.006
44. Caragata EP, Dutra HLC, Sucupira PHF, Ferreira AGA, Moreira LA. Wolbachia as translational science: controlling mosquito-borne pathogens. Trends Parasitol. 2021 Dec;37(12):1050–67. doi:10.1016/j.pt.2021.06.007
45. Gong JT, Li TP, Wang MK, Hong XY. Wolbachia-based strategies for control of agricultural pests. Curr Opin Insect Sci. 2023 Jun;57:101039. doi:10.1016/j.cois.2023.101039
46. Nguyen PN, Rehan SM. Environmental Effects on Bee Microbiota. Microb Ecol. 2023 Oct 26;86(3):1487–98. doi:10.1007/s00248-023-02226-6
47.* Motta EVS, Moran NA. The honeybee microbiota and its impact on health and disease. Nat Rev Microbiol. 2024 Mar 4;22(3):122–37. doi:10.1038/s41579-023-00990-3

Reviews how stable host-adapted gut microbiota are assembled and maintained in honeybees, providing a model system for specialized insect microbiomes.

48.* Ravenscraft A, Coon KL. Transient Microbes in Insects: Fleeting but Functional. Annu Rev Entomol. 2026 Jan 28;71(1):253–73. doi:10.1146/annurev-ento-121423-013446

Challenges the traditional view that environmentally acquired microbes are ecologically unimportant, highlighting the functional significance of transient insect microbiota.

49. Pedroncelli A, Singh Y, Hogenhout SA, Janik K. Advances in Understanding Phytoplasma Interactions with Plants and Insects. Annu Rev Phytopathol. 2026 May 11. doi:10.1146/annurev-phyto-011325-105751

50. Heck M. Insect Transmission of Plant Pathogens: a Systems Biology Perspective. mSystems. 2018 Apr 24;3(2). doi:10.1128/mSystems.00168-17