Phylosymbiotic Relationship between Insects and Symbionts

Subjects: Entomology Contributor: Man Qin, Liyun Jiang, Gexia Qiao, Jing Chen

Insects harbor diverse assemblages of bacterial and fungal symbionts, which play crucial roles in host life history. Insects and their various symbionts represent a good model for studying host–microbe interactions. Phylosymbiosis is used to describe an eco-evolutionary pattern, providing a new cross-system trend in the research of host-associated microbiota. The phylosymbiosis pattern is characterized by a significant positive correlation between the host phylogeny and microbial community dissimilarities.

Keywords: microbial community structure ; phylosymbiosis pattern ; stochastic effect ; codiversification ; ecological filtering

1. Introduction of Phylosymbiosis

Host–microbe symbioses play a crucial role in the ecological and evolutionary history of animals ^{[1][2]}. Recent advances in the field of host–microbe interactions have demonstrated the influence of host phylogeny and ecological factors on microbial community assembly ^{[3][4][5]}. Phylosymbiosis occurs when host-associated microbiota relationships are positively associated with host phylogenetic relatedness.

Phylosymbiosis is defined as "microbial community relationship parallels the host phylogeny", in which "phylo" refers to host lineage and "symbiosis" refers to the coexistence of hosts and microbes (**Figure 1**) ^{[G][\mathcal{I}]}. In other words, microbial community composition dissimilarities are positively associated with the accumulation of host genetic variation. Phylosymbiosis studies focus on the entire microbiota rather than individuals within the microbiota. The persistent and intimate association between microbes and their host is not the necessary assumption of this eco-evolutionary pattern ^[8].

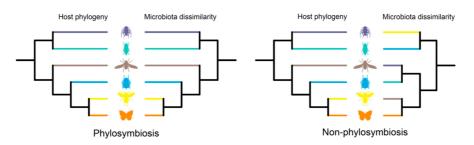


Figure 1. Phylosymbiotic versus stochastic microbial community assemblages. Branches in the same color indicate the host and associated microbial community.

Pioneering studies on phylosymbiosis were performed on the parasitoid wasp genus *Nasonia* under rearing conditions ^[9], in which species-specific phylosymbiotic gut bacterial communities caused lethality in interspecific hybrids ^[I]. Afterward, Brooks et al. ^[10] revealed phylosymbiosis in other animals, including deer mice (*Peromyscus*), fruit flies (*Drosophila*), and mosquitoes (i.e., *Anopheles*, *Aedes*, and *Culex*). To date, interspecific phylosymbiotic structures of microbiota have been widely reported in insects, birds, fishes, and mammals ^{[5][10][11][12][13][14][15][16][17][18]}. However, phylosymbiosis remains poorly understood at the intraspecific level. Intraspecific phylosymbiosis has only been substantiated in the microbial communities from the American pika *Ochotona princeps* ^[19] and the aphid *Mollitrichosiphum tenuicorpus* ^[20]. The host taxa in insect phylosymbiosis studies to date cover orders, families, genera, and species, and the evolutionary history of hosts spans approximately 0.3–300 million years ^{[6][21]}. The strength of the phylosymbiotic signals between the host and microbiota varies across host taxa ^[8], and the phylosymbiotic relationships can be weakened with an increasing host evolutionary history ^{[5][21]}.

Phylosymbiosis analyses typically employ 16S rRNA gene amplicon sequencing data as the input data of the microbial community. Multiple beta diversity distance metrics are usually required for the robustness of the results ^[8]. Furthermore,

a reliable host phylogenetic tree is essential for the determination of phylosymbiosis patterns. The key to measuring phylosymbiosis is to assess the significant correlation between host phylogeny and microbiota beta diversity. Principal methods for quantifying phylosymbiosis are as follows: (1) topological congruency tests ^[10] utilizing the Robinson–Foulds metric ^[22] or matching cluster metric ^[23], or (2) a matrix correlation-based approach, e.g., the Mantel test ^[24] and Procrustean superimposition ^[25].

2. Phylosymbiosis in Insects

Insects constitute the most diverse group of animals and play crucial roles in terrestrial ecosystems ^[26]. Insects harbor a great variety of symbionts, which contribute significantly to the survival, growth, and fecundity of the host ^{[2][27][28]}. Additionally, symbionts could facilitate host adaptation to new ecological niches and potentially drive speciation in insects ^{[1][29]}. Insect microbial community structures have been found to be correlated with environmental habitat, diet, sex, life stage, and host insect identity and phylogeny ^{[30][31][32]}. Some studies highlighted the strongest impact of insect species on the associated microbial communities ^{[30][33]}. Currently, phylosymbiosis research in insects remains in its infancy, and phylosymbiosis has been confirmed in the orders Blattodea, Coleoptera, Diptera, Isoptera, Hemiptera, and Hymenoptera **(Table 1)**.

Insects Examined		No. of Species Sampled	Evolutionary Time (Mya)	Diet	Core Microbe	Obligate Symbiont	References
Blattodea		19	>300	Omnivory	Bacteroidetes, Firmicutes, and Proteobacteria	_	[21]
Coleoptera	Dendroctonus frontalis species complex	7	12	Phloem cell	Ceratocystiopsis	_	<u>[34][35]</u>
Diptera	Anopheles, Aedes, and Culex	8	100	Blood	Proteobacteria	_	[<u>10][36]</u>
	Drosophila	6	63	Decaying fruit	Proteobacteria	_	[10]
Hemiptera	Greenideinae	53	83	Phloem sap	_	Buchnera aphidicola	[<u>37][38]</u>
	Mollitrichosiphum	8	18–19	Phloem sap	_	Buchnera aphidicola	[33]
	Mollitrichosiphum tenuicorpus	1 (26 colonies)	11	Phloem sap	_	Buchnera aphidicola	[20]
	Psylloidea	102	350	Phloem sap	_	Carsonella ruddii	[<u>39][40]</u>
Hymenoptera	Cephalotes	13	46	Pollen and honeydew	_	Cephaloticoccus	[41]

Insects Examined	I	No. of Species Sampled	Evolutionary Time (Mya)	Diet	Core Microbe	Obligate Symbiont	References
	Ceratosolen	6	60	Fig	Wolbachia	_	[42][43]
	Formica	14	30	Honeydew and nectar	Wolbachia, Lactobacillus, Liliensternia, and Spiroplasma		[44][45]
	Nasonia	4	<1	Fly puparium	Proteobacteria, Firmicutes, and Actinobacteria	_	[10]
Lepidoptera					Acinetobacter, Apibacter, Asaia,		
	Heliconiini	23	20–30	Pollen, nectar,	Commensalibacter, Enterobacter, Enterococcus,		[46][47]
References				and fruit	Lactococcus,		

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In most animal systems, microbial transmission and host filtering are major factors influencing microbial community 5. Groussing Marcel, F.: Sanders, J.G.: Smillie, C.S.: Lavergne, S.: Thuiller, W.: Alm, E.J. Unraveling the processes assembly in the maintenance of microbes within insect populations usually relies on vertical and horizontal shaping mammalian gut microbiomes over evolutionary time. Nat. Commun. 2017, 8, 14319. transmission. Strict vertical transmission can promote host-microbe codiversification and ensure the high fidelity of close hostimaisrebie asseeting asseeting asseeting antony evolutionally exercise for the high fidelity of close fostimaisrebie asseeting and horizontal transmission can promote host-microbe codiversification and ensure the high fidelity of close fostimaisrebie asseeting and antony evolution and the second device of the second devoce device of the second device of

transmissions between different host species may weaken the stability of long-lasting host-microbe associations and 8. Mazel, F.; Davis, K.M.; Loudon, A.; Kwong, W.K.; Groussin, M.; Parfrey, L.W. Is host filtering the main driver of obscure the phylosymbiotic signatures of microbial communities. For example, significant phylogenetic correlations were phylosymbiosis across the tree of life? mSystems 2018, 3, e00097-18. not found within the bacterial communities of heteroecious aphids, in which frequent horizontal transmissions of secondary, symbiotic management of the role solution and the species and development shapes microbial communities. Evolution 2012, 66, 349-362 microbial communities, namely, microorganism filtration within the host. One is the species assortment assembly process,

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Here, the researchers summarize the contributions of stochastic effects and deterministic forces (i.e., evolutionary and/or

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Figure 2. Mechanisms underlying phylosymbiosis. (A) Gain or loss of microbes arises from stochastic processes. (B)

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26. Basset, Y.; Cizek, L.; Cuénoud, P.; Didham, R.K.; Guilhaumon, F.; Missa, O.; Novotny, V.; Ødegaard, F.; Roslin, T.;
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27hplenmultiotici.miceologietascen, 193; Fa. Miceonyanceme introductional associational inductional neurophylocity of the second se and 8 a 8 d o b 11 fluctuations in the abundance of microbes (Figure 2A) [56]. Dispersal is referred to as the movement and 28. Douglas, A.E. Mycelocyte symbols in insects. Biol. Rev. 1589, 64, 409–434. could promote the compositional divergence of gut microbial communities among mammalian species. In addition to 29. Sudakaran, S.; Kost, C.; Kaltenpoth, M. Symbiont acquisition and replacement as a source of ecological innovation spatial limitations, the composition of the microbial community can be disturbed by the rate and order of microbes that are added to the microbiola during dispersal processes ^[59]. The microbial dispersal associated with insects generally occurs 370. Malaxiiade Aultostappasissoidentity slopes incluing servand stance acquister, northological advised and a contract and a contract of the standard and a contract o smeaning of the egg surface, and capsule or jelly-like secretion transmission [60].

31. Huang, K.G.; Wang, J.; Huang, J.H.; Zhang, S.K.; Vogler, A.P.; Liu, Q.Q.; Li, Y.C.; Yang, M.W.; Li, Y.; Zhou, X.G. Host Ecological drift leads to random variation in the relative abundance of species within the microbial community over time phylogeny and diet shape gut microbial communities within bamboo–leeding insects. Front. Microbiol. 2021, 12,

1611 6 Min provide the subsequent extinction. Ecological drift can generate differences in microbial community composition when deterministic processes are weak [59]. In insects, microbiota profiling Service and the service of the service

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Zúñiga, G. Metabarcoding of mycetangia from the Dendroctonus frontalis species complex (Curculionidae: Scolytinae) 3.2e Exal utionser and token and redundant fungal assemblages. Front. Microbiol. 2022, 13, 969230.

35nyilasylmbilosisCcanataseAroAnobYgl-tenk aRabaalia Rszocharions Berwelerwnicebeellantanbsta, Sachrasteebeotrantaniand (Coleoptera: Curculionidae: Scolytinae) reveal an east-west genetic subdivision of early Pleistocene prigin Insect Syst simultaneity of evolutionary changes in interacting species [63]. Cospeciation can result from coevolution and occurs when 360 shovakidvaniEroldeso sheeriateD. Sim Reatriguesty Right o Derivon Braciker, Red. cdeet foldt. Waharian As; Amir, Ayn Knieghts, Rinder confronted constructions with provide a packground because a construction of the second construction o util Mingo biny lage 7 and genomic analyses, we can deduce insect-symbiont coevolution [65][66]. Insects feeding on 37h LOAM NARCERER AS A REAL AS A REAL AND A

in theirithedesevinee of the biosynthetic and metabolic

complementarity of essential nutrition to maintain intimate associations ^{[29][69][70][71]}. For instance, the primary 38. Liu, Q.H.; Chen, J.; Huang, X.L.; Jiang, L.Y.; Qiao, G.X. Ancient association with Fagaceae in the aphid tribe endosymbiont. *Buchnera aphidicola* has highly coadapted to and evolved with aphids for millions of years ^{[72][73][74]}. Greenideini (Hemiptera: Aphididae. Greenideinae). Syst. Entomol. 2015, 40, 230–241. Likewise, such coevolutionary examples have been identified from extracellular gut symbionts that enable nutrient

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stinhagterial and the microbiome of psyllids (Hemiptera: Psylloidea) in Aotearoa New Zealand. PLoS ONE 2023, 18, e0285587.

Codiversification represents another evolutionary process that underlies phylosymbiosis (Figure 2B). It occurs when hosts 40. Johnson, K.P.; Dietrich, C.H.; Friedrich, F.; Beutel, R.G.; Wipfler, B.; Peters, R.S.; Allen, J.M.; Petersen, M.; Donath, A.; and white R best extended by the set of the Codiversification can be a consequence of unidirectional selection; that is, microbes adapt to the evolutionary changes

imposed by their hosts but not vice versa. In the social corbiculate bees, a strain-level phylogenetic association between 41. Hu, Y. D'Amelio, C.L.; Béchade, B.; Cabuslay, C.S.; Łukasik, P.; Sanders, J.G.; Price, S.; Fanwick, E.; Powell, S.; the core gut bacteria *Lactobacillus* Firm-5 and the host bees was observed, which suggested host-microbe Moreau, C.S.; et al. Partner fidelity and environmental filtering preserve stage-specific turtle ant gut symbioses for over codiversification ¹²⁹. Other adaptation processes, such as host-shift speciation ¹²⁹ and shared geographic isolation 40 million years. Ecol. Monogr. 2023, 93, e1560. can also contribute to matching phylogenies of microbes and host lineages.

42. Li, J.; Wei, X.; Huang, D.W.; Xiao, J. The phylosymbiosis pattern between the fig wasps of the same genus and their

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community assembly, which is referred to as priority effects [81]. The importance of priority effects in shaping microbial 44. Jackson, R.; Patapiou, P.A.; Golding, G.; Helanterä, H.; Economou, C.K.; Chapuisat, M.; Henry, L.M. Evidence of community composition has been reviewed [82]. Moreover, multiple studies have revealed that highly connected keystone phylosymbiosis in Formica ants. Front. Microbiol. 2023, 14, 1044286.
 or hub microbes can determine the overall community structure via interspecific interactions [83][84][85].

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transmitted to offspring paternally via an intrasperm passage as well as maternally via an ovarial passage [88]. Additionally, 47. Cicconardi, F.; Milanetti, E.; Pinheiro de Castro, E.C.; Mazo-Vargas, A.; Van Belleghem, S.M.; Ruggieti, A.A.; Rastas, some axtracellular and a simplights, carbe and enable that with the some of yprotechartie in the analytic stinker with the bigs of a standard with the bigs of a st

e.g., *Acromyrmex* leaf-cutting ants ^[90] and the honey bee *Apis mellifera* ^[91], social acquisition of beneficial microbes is 48. Mallott, E.K.; Amato, K.R. Host specificity of the gut microbiome. Nat. Rev. Microbiol. 2021, 19, 639–653. critical for specificity and partner fidelity in host-bacterial associations. These initial colonizing symbionts with vertical

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microbes and then yield phylosymbiotic microbiota. Closely related hosts have similar physiological characteristics, 53. Cornwell, W.K.; Schwilk, D.W.; Ackerly, D.D. A trait-based test for habitat filtering: Convex hull volume. Ecology 2006, immune systems, or microbial defense mechanisms [89][92][93][94], which may bring about the tendency to harbor similar 87, 1465–1471. microbial communities

54 the ecological take of that shade microbiotanstructures are worked by phytophological dispersive and the fost evolutionary history, we can observe a phylosymbiotic relationship between the host and microbiota ^[8]. Here, the researchers provide

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level assembly rules. Proc. Natl. Acad. Sci. USA 2013, 110, 12804–12809.

3.3.1. Immune System

56. Kohl, K.D. Ecological and evolutionary mechanisms underlying patterns of phylosymbiosis in host-associated microbial Nuther free states and the states of the second of the sec

composition [95][96][97][98]. Insects rely on physiological barriers and innate immune responses to defend themselves 57. Hanson, C.A.; Fuhrman, J.A.; Horner-Devine, M.C.; Martiny, J.B. Beyond biogeographic patterns: Processes shaping against pathogens [99][100]. The innate immune system of insects is composed of cellular immune responses by circulating the microbral landscape. Nat. Rev. Microbiol. 2012, 10, 497–506. hemocytes [101] and humoral immune responses. Although the hemocyte categories involved in cellular immune function of the process of the process of the hemocyte categories involved in cellular immune 58 sponses Adry Surouky Tuffereint Instact species; Wasserve Krunkachmannima Wy Dispected limitation of and diversification <u>hogithermanian</u> gut microbiota. Proc. Natl. Acad. Sci. USA 2017, 114, 13768–13773. encapsulation <u>hogithermanian</u>. Humoral defenses are modulated by the Toll, immune deficiency (IMD), Jun N-terminal kinase 591.NKgmetagutsDkRna&elsigidal Srknselukænsi, and 'bleikladors; bilindanscrivbtionar(idak/LSFLAK);elandin,plotphetadoxidaseLyPerQ) pathwaysviewellyon, the Rattesson drp pares an anois of the relation of the second provided and the se protification protification, and melanization. Insects depend on two pathways to regulate 62ntispierapial; papticle, percentions, namely the Jall, pathway which do support the transference of the particular and the Manastriwa of which drain d weeter a first and weeter and the sector of the sector

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are more similar among closely related bee species ^[78]. The exotic strain of the gut symbiont *Gilliamella* in honey bees 64. Hoberg, E.P.; Brooks, D.R.; Siegel-Causey, D. Host-parasite co-speciation: History, principles, and prospects. In Host-induced higher prostaglandin (PG) production than the native strain, which increased the expression of genes in the IMD Parasite Evolution: General Principles and Avian Models; Clayton, D.H., Moore, J., Eds.; Oxford University Press: New and Toll immune pathways ^[13]. These immune pathways then modulated the dual oxidase (Duox) production and ROS York, NY, USA, 1997; pp. 212–235. generation to inhibit the nonnative strain of *Gilliamella*.

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filtered by diet ^[31]. If diets themselves are phylogenetically nonindependent, they can serve as ecological filters and lead 68. Sandström, J.; Moran, N.A. How nutritionally imbalanced is phloem sap for aphids? Entomol. Exp. Appl. 1999, 91, 203– to phylosymbiotic microbiota. Moreover, complete dietary shifts over long evolutionary periods can disrupt the 210. 68

phylosymbiotic relationship between host and microbial communities ^[5].

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members of the adult-stage gut microbiota in butterflies are abundant and consistent ^[46]. The phylosymbiotic signature of 70. Luan, J.B.; Chen, W.B.; Hasegawa, D.K.; Simmons, A.M.; Wintermantel, W.M.; Ling, K.S.; Fei, Z.J.; Liu, S.S.; Douglas, microbiota within beliconing butterflies mere size from the filter microbiota wibbin believolution hyther basterial sying icross of the fillening and phyloge platic stap regaring research provide the second states of the se Within appids, host symbolic conversification as well as filtering by host plants has been highlighted in structuring the

phylosymbiotic microbiota of Greenideinae species ^[37]. 71. Russell, C.W.; Bouvaine, S.; Newell, P.D.; Douglas, A.E. Shared metabolic pathways in a coevolved insect–bacterial 3.3sgn Pringsito Koppic all Ichinana differintics. 2013, 79, 6117-6123.

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