HOKKAIDO UNIVERSITY

Title	Integrative insights into novel host range expansion in the Solidago-specialist invasive aphid Uroleucon nigrotuberculatum
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Description	この博士論文の全文は利用可能日以降に公開されます。
Degree Grantor	北海道大学
Degree Name	博士(環境科学)
Dissertation Number	乙第7229号
Issue Date	2025-12-25
DOI	https://doi.org/10.14943/doctoral.r7229
Doc URL	https://hdl.handle.net/2115/98674
Type	doctoral thesis
File Information	ILYAS_Amna_abstract.pdf, 論文内容の要旨 https://creativecommons.org/licenses/by/4.0/

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学 位 論 文 内 容 の 要 旨/Dissertation Abstract

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学 位 論 文 題 名/Title of Dissertation

Integrative insights into novel host range expansion in the *Solidago*-specialist invasive aphid *Uroleucon nigrotuberculatum*

（*Solidago*属スペシャリストの侵入アブラムシ*Uroleucon nigrotuberculatum*における新規寄主幅拡大に関する統合的洞察）

In the Anthropocene, biological invasions have intensified, with species moving beyond their native ranges. These invasions often include plants and their associated herbivores, which establish, expand, and sometimes become invasive. Lacking shared evolutionary history with native communities, exotic herbivores form novel interactions, but how these interactions are formed the mechanisms remain unclear. Since most herbivorous insects are dietary specialists, a key question arises: how does a monophagous herbivore, which in its native range is strictly associated with one host species, succeed in expanding its host range in a new region? Therefore, I conducted this research to investigate the host range expansion of the invasive aphid *Uroleucon nigrotuberculatum*, which is a *Solidago* specialist in the native region, North America. Introduced to Japan following the introduction of *Solidago altissima*, it has also been recorded only on *Solidago altissima*, despite the presence of other native *Solidago virgurea* and exotic *Solidago gigantea* in Japan. Recently, similar red aphids were observed on Asteraceae in Hokkaido, suggesting host range expansion of this aphid. The goal of my dissertation is to test the natural pattern of the host range expansion and explore its driving factors. Following the general introduction, I conducted three studies, which are detailed in chapters two, three, and four, respectively. The second chapter of my thesis tested whether aphids found on multiple Asteraceae in Hokkaido were the Solidago specialist *U. nigrotuberculatum*. I collected colonies from *S. altissima*, *Taraxacum officinale*, and *Senecio vulgaris* in Hokkaido, and from *S. altissima* in Shiga and Yokohama. Phylogenetic and morphological analyses confirmed all samples as *U. nigrotuberculatum*, with no genetic differences between aphids from novel hosts and those from *S. altissima*. Inoculation experiments further showed that aphids from *S. altissima* could survive and reproduce on *S. gigantea*, *T. officinale*, and *S. vulgaris*, providing strong evidence of host range expansion in Japan. These results highlight the species' ability to exploit new plants, supporting its potential for further spread.In the third chapter, I investigated the host range expansion of this aphid by using a common garden experiment to examine the ecological mechanisms that promote this host range expansion from the primary host (*S. altissima*) to the novel host (*T. officinale*) by focusing on the role of genetic diversity and recipient plant condition in facilitating spillover and host range expansion. Here, I addressed 1) Can *U. nigrotuberculatum* spill over from *S. altissima* to *T. officinale* when the two are grown together? 2) Does higher aphid density on the host plant increase the likelihood of spillover from *S. altissima* to *T. officinale*? (iii) Is aphid density better explained by host plant genotype identity or by host genotypic diversity? (iv) *Does the status of T. officinale (bolting vs. non-bolting) affect the likelihood of U. nigrotuberculatum colonization?* To examine this, I manipulated the genotypic diversity of *S. altissima* populations, using both single-genotype and mixed-genotype treatments, and paired each plot with *T. officinale*. I investigated the naturally colonized aphid numbers on each plant

twice a week from July to mid-October. As a result, I found that *U. nigrotuberculatum* successfully colonized both *S. altissima* and *T. officinale*. Early in the season, higher aphid densities on *S. altissima* increased the likelihood of colonization on *T. officinale*. In the late season, colonization on *T. officinale* was consistently high because the aphid density was extremely high across all *S. altissima* individuals. Aphid abundance on *S. altissima* significantly varied among plant genotypes in both early and late season, while overall genotypic diversity (single vs. mixed) had no significant effects. These results suggest that the aphids' spillover patterns were shaped more by which genotype was present than by the number of genotypes. Recipient plant condition also played a crucial role to complete a novel host colonization: only bolting *T. officinale* supported successful colonization, while non-bolting plants were never colonized. These results showed that host range expansion is driven by multiple interacting factors: aphid density on the primary host, host genotypes, and recipient plant condition, all of which shape the likelihood and success of colonization on novel hosts. In particular, the importance of recipient plant condition indicates that not only density-dependent emigration from primary host (i.e., a passive process) but also ecological fitting with recipient plants (i.e., adaptive foraging) are important in the host range expansion. In the fourth chapter, I investigated the patterns of the aphid's symbiont microbiome among different plant species to obtain insights into whether symbionts can be associated with host usage habits because aphids harbor diverse bacterial communities that can influence their survival, nutrition, and adaptation to host plants. I hypothesized that aphids from the primary host (*S. altissima*) and novel hosts would harbor distinct microbiomes. To test this, I conducted two experiments. First, an inoculation experiment was carried out. Aphid colonies from *S. altissima* were transferred onto *S. gigantea* and *S. altissima* experimental plants and maintained under mesh cages for 2–3 weeks. Second, I collected natural aphid colonies from *S. altissima*, *S. gigantea*, *T. officinale*, *S. vulgaris*, and *C. album* in Sapporo, as well as *S. altissima* from Yokohama, all of which occurred naturally in the field. This design allowed me to compare microbial communities both experimentally and across geographically distinct field populations. I asked two questions: 1) Does the microbiome composition shift after inoculation to novel hosts? 2) Do aphids from novel hosts in the field harbor microbiomes distinct from those on *S. altissima*? Microbial communities were characterized using 16S rDNA amplicon sequencing. Results revealed that host plant identity influenced aphid microbiomes. Inoculated aphids showed differences in ASV richness and composition compared to pre-inoculation colonies. Inoculated aphid populations on *S. altissima* and *S. gigantea* also tended to show divergent microbial communities, while no significant difference was found due to high variability among samples. Field-collected samples showed significant differences in bacterial community composition across host species and geographic locations. These findings demonstrate that microbiomes reorganized on different plants on a very short time scale, indicating that microbiome dynamics may contribute to early stages of host expansion. In the final chapter, I synthesized the above studies. Collectively, these integrated studies provided the first-ever evidence for the host range expansion and its underlying mechanism for the monophagous specialist aphid in the introduced region. Extreme high density in the introduced region, which may have resulted from the release of competitors and natural enemies, and recent climate changes, promoted this novel host range expansion. Moreover, most of the novel hosts used by this aphid were introduced plant species. Globally accelerating invasion could lead to the development of a wide range of unpredictable, novel interactions in the introduced range. However, this doesn't mean rapid evolutionary changes always occur. Pre-adaptation (i.e., ecological fitting) and labile symbionts may contribute to novel host range expansion. Overall, my findings advance our understanding of how invasive insects adapt to novel environments and provide broader implications for invasion ecology.