



PHYTOPHAGOUS INSECT ASSEMBLAGES ON NATIVE AND INTRODUCED GYMNOSPERMS ACROSS AN ECOTOPIC GRADIENT IN FERGANA VALLEY

Gulnorakhon ZOKIROVA^{1,*}

¹ Department of Zoology, Fergana State University, Murabbiylar Street 19, 150100 Fergana, Uzbekistan

g.zokirova80@gmail.com; ORCID: 0009-0007-9504-8072

Abstract: Gymnosperms of Central Asia, comprising native *Juniperus*, *Ephedra* and *Picea* taxa together with a growing array of ornamental introductions, support a poorly resolved community of phytophagous insects. We surveyed phytophagous insects across four contrasting ecotopes (urban ecosystems, semi-arid foothills (adir), piedmont juniper woodlands and montane forests) in eastern Uzbekistan and the adjacent south-western provinces of the Kyrgyz Republic between 2022 and 2026. A total of 72 phytophagous insect species were associated with 17 native and introduced gymnosperm taxa. Host plants partitioned into three diversity groups: low (2–5 species; *Ephedra* spp., *Juniperus semiglobosa*, *J. virginiana*, *Abies* spp., *Cupressus* spp.), medium (8–12 species; *Picea schrenkiana*, *J. sabina*, *J. turkestanica*, *Thuja occidentalis*, *Platycladus orientalis*) and high (17–28 species; *Pinus sylvestris*, *P. nigra* subsp. *pallasiana*, *P. brutia* var. *eldarica*, *Juniperus seravschanica*). Introduced *Pinus* plantations and the widely distributed native *J. seravschanica* supported the richest assemblages. Adventive aphids (*Cinara palaestinensis*, *C. pinimaritimae*) and the leaf-footed conifer seed bug *Leptoglossus occidentalis* recorded from the region demonstrate ongoing invasion processes mediated by ornamental plantings. Our results clarify the ecotopic structuring of conifer-feeding insect assemblages in Central Asia and emphasise the role of urban gymnosperm plantings as bridgeheads for alien pests.

Keywords: Central Asia; Cupressaceae; Pinaceae; *Ephedra*; alien insects; conifer pests; ecotopic gradient; biological invasions; Fergana Valley

1. Introduction

Gymnosperms occupy a central place in the vegetation cover of Central Asia, where



they form the upper-storey of arid and semi-arid mountain forests and structure unique ecosystems that have evolved over long geological timescales [1–3]. Native conifers and gnetophytes of the region—chiefly *Juniperus seravschanica* Kom., *J. semiglobosa* Regel, *J. turkestanica* Kom., *J. sabina* L., *Picea schrenkiana* Fisch. & C.A.Mey. and several *Ephedra* species—provide the dominant biomass of upland ecotopes, while a growing array of introduced Pinaceae and Cupressaceae has been planted in urban and agroforestry settings since the late 19th century [4,5].

Gymnosperm hosts support specialised guilds of phytophagous insects whose composition reflects both deep co-evolutionary history and recent human-mediated introductions [6,7]. In Europe and North America the conifer-associated entomofauna has been studied in detail, including the consequences of host range expansion by bark beetles, scale insects and lepidopteran defoliators [8–10]. Recent works also document an accelerating wave of invasive conifer-feeding insects in urban green spaces, where introduced ornamental hosts act as bridgeheads for alien herbivores [11–13]. For Central Asia, however, comprehensive accounts of the phytophagous fauna of gymnosperms remain scarce and largely scattered through grey literature [14,15].

Eastern Uzbekistan and the adjacent south-western provinces of the Kyrgyz Republic encompass an exceptionally steep ecological gradient. Within a few tens of kilometres the landscape passes from intensely managed lowland urban ecosystems through *adir* (semi-arid foothills dominated by *Ephedra* shrublands), into piedmont juniper woodlands and finally to montane forests of *Juniperus* and *Picea schrenkiana* [3,16]. Each ecotope offers a different host-plant palette, climatic regime and degree of human disturbance, providing an opportunity to test how phytophagous insect assemblages partition along an environmental gradient that combines native and introduced hosts at every step.



Three observations motivated the present survey. First, the broad host spectrum of ornamental Pinaceae planted in regional cities—including *Pinus sylvestris* L., *P. nigra* J.F.Arnold subsp. *pallasiana* (Lamb.) Holmboe and *P. brutia* Ten. var. *eldarica* (Medw.) Silba—has rarely been examined as a single entomological unit. Second, recent records of the alien aphids *Cinara palaestinensis* Hille Ris Lambers and *C. pinimaritimae* (Dufour) from urban *Pinus* in the Fergana Valley [17] suggest that the region is actively accumulating adventive conifer pests. Third, the lack of a synthetic, host-resolved checklist hampers both biodiversity assessment and early detection of emerging invasions.

Here we provide a synthesis of phytophagous insect assemblages associated with 17 native and introduced gymnosperm taxa across four ecotopes of eastern Uzbekistan and adjacent Kyrgyzstan, based on field surveys carried out from 2022 to 2026. Specifically, we (i) quantify host-plant species richness and the proportional contribution of each host to the regional entomofauna; (ii) identify host-plant groups characterised by low, medium and high insect richness; and (iii) discuss the role of introduced ornamental conifers as hosts for both native polyphagous and adventive insect species. The results provide a baseline against which future invasions and climate-driven range shifts can be assessed.

2. Materials and Methods

2.1. Study area and ecotopes

Field surveys were conducted between 2022 and 2026 across the eastern part of the Republic of Uzbekistan (Fergana, Andijan, Namangan and Tashkent provinces) and the contiguous south-western provinces of the Kyrgyz Republic (Batken, Osh, Jalal-Abad), covering an elevational span of approximately 300–2800 m a.s.l. Four major ecotopes were sampled and treated as the structural units of the analysis (Figure 1):

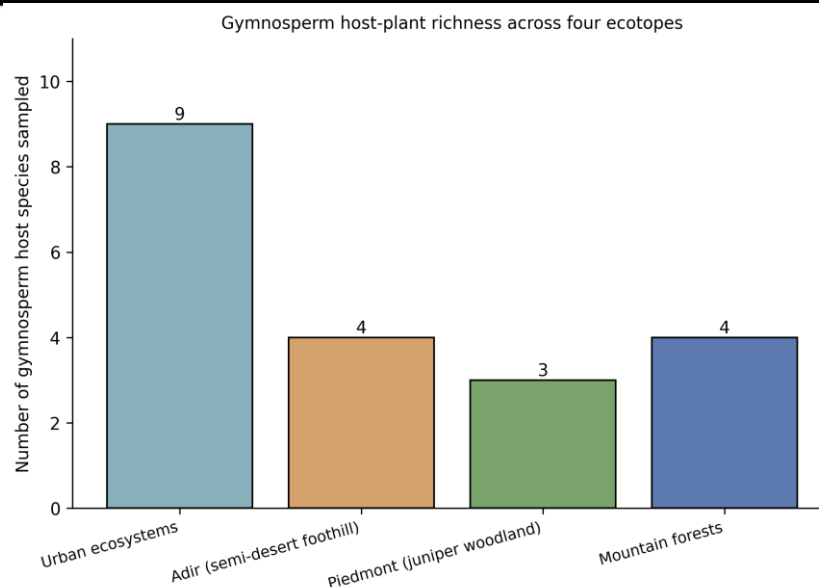


Figure 1. Gymnosperm host-plant richness in the four ecotopes (urban ecosystems, adir, piedmont juniper woodlands, mountain forests). Urban ecotopes are dominated by introduced ornamental conifers, whereas piedmont and mountain ecotopes are dominated by native *Juniperus* and *Picea schrenkiana*.

Urban ecosystems — squares, parks and street plantings in regional cities. Dominant hosts were ornamental introductions: *Thuja occidentalis* L., *Platycladus orientalis* (L.) Franco, *Pinus nigra* subsp. *pallasiana*, *P. brutia* var. *eldarica*, *P. sylvestris*, *Abies sibirica* Ledeb., *Picea* spp., *Cupressus* spp. and *Juniperus virginiana* L.

Adir (semi-arid lowland foothill steppe) — sparse xerophytic shrub communities in which the trophic substrate for phytophages was provided mainly by *Ephedra equisetina* Bunge, *E. intermedia* Schrenk & C.A.Mey., *E. distachya* L. and locally by *Juniperus sabina*.

Piedmont (foothill) juniper woodlands — open archa stands of *Juniperus seravschanica*, *J. semiglobosa* and *J. turkestanica* forming the principal native gymnosperm communities of the region.

Mountain forests — closed-canopy archa woodlands and *Picea schrenkiana* stands at higher elevations, where the same *Juniperus* species occur in their climax form.

2.2. Sampling design

Across the four ecotopes, 17 host gymnosperm taxa were sampled (Table 1). At each site between three and ten host individuals per species were inspected per visit, depending on local abundance. Insects were collected from foliage, branches, cones, bark and root collar by visual searching, beating onto a 1 × 1 m white sheet, sweep-netting of associated herbaceous understorey, and by attended yellow pan-traps placed for 24 h within the canopy projection. Bark and cone material from senescent or wind-fallen branches was reared in ventilated laboratory containers (20–25 °C; 50–60 % RH) until adult emergence. Sampling was repeated through the active season (March–October) of each year, yielding a total of more than 600 host-individual inspections during 2022–2026.

Table 1. Phytophagous insect species richness associated with native and introduced gymnosperms in eastern Uzbekistan and adjacent Kyrgyzstan (2022–2026). Group I = low richness (2–5 spp.); Group II = medium (8–12 spp.); Group III = high (17–28 spp.). Total regional phytophagous fauna recorded across the study, $n = 72$ species.

Host plant	Group	Status	Main ecotope(s)	Insect spp.	% of total
<i>Pinus sylvestris</i>	III	Introduced	Urban	28	38.9
<i>Pinus nigra subsp. pallasiana</i>	III	Introduced	Urban	22	30.6
<i>Juniperus seravschanica</i>	III	Native	Piedmont, mountain	19	26.4
<i>Pinus brutia var. eldarica</i>	III	Introduced	Urban	17	23.6
<i>Thuja occidentalis</i>	II	Introduced	Urban	12	16.7
<i>Juniperus turkestanica</i>	II	Native	Piedmont, mountain	12	16.7
<i>Juniperus sabina</i>	II	Native	Adir, piedmont	11	15.3
<i>Platycladus orientalis</i>	II	Introduced	Urban	11	15.3

Host plant	Group	Status	Main ecotope(s)	Insect spp.	% of total
<i>Picea schrenkiana</i>	II	Native	Mountain	8	11.1
<i>Pinus spp. (other)</i>	I	Introduced	Urban	5	6.9
<i>Ephedra equisetina</i>	I	Native	Adir	4	5.6
<i>Ephedra distachya</i>	I	Native	Adir	4	5.6
<i>Juniperus semiglobosa</i>	I	Native	Piedmont	4	5.6
<i>Abies spp.</i>	I	Introduced	Urban	4	5.6
<i>Cupressus spp.</i>	I	Introduced	Urban	4	5.6
<i>Ephedra intermedia</i>	I	Native	Adir	2	2.8
<i>Juniperus virginiana</i>	I	Introduced	Urban	2	2.8

2.3. Identification and data analysis

Adult insects were identified to species level using standard regional and Palaearctic keys for Hemiptera (Aphididae, Coreidae, Pseudococcidae, Diaspididae, Coccidae), Coleoptera (Curculionidae: Scolytinae, Buprestidae, Cerambycidae, Chrysomelidae), Lepidoptera (Tortricidae, Geometridae, Lasiocampidae, Erebididae) and Hymenoptera (Diprionidae). DNA barcoding of the mitochondrial COI gene was used to confirm the identity of cryptic or recently introduced taxa, including the two adventive *Cinara* species [17].

For each host-plant species the total number of phytophagous insect species recorded across the study period was calculated, and the proportional share of the regional entomofauna ($n = 72$) was expressed as a percentage. Host plants were then assigned to three operational diversity groups using natural breaks in the observed distribution: low (2–5 species), medium (8–12 species) and high (17–28 species).

3. Results

3.1. Overall richness and host-plant grouping

A total of 72 phytophagous insect species were recorded in association with 17 gymnosperm taxa across the four ecotopes of eastern Uzbekistan and adjacent Kyrgyzstan (Figure 2; Table 1). Host plants segregated into three diversity groups corresponding to clearly different patterns of trophic association.

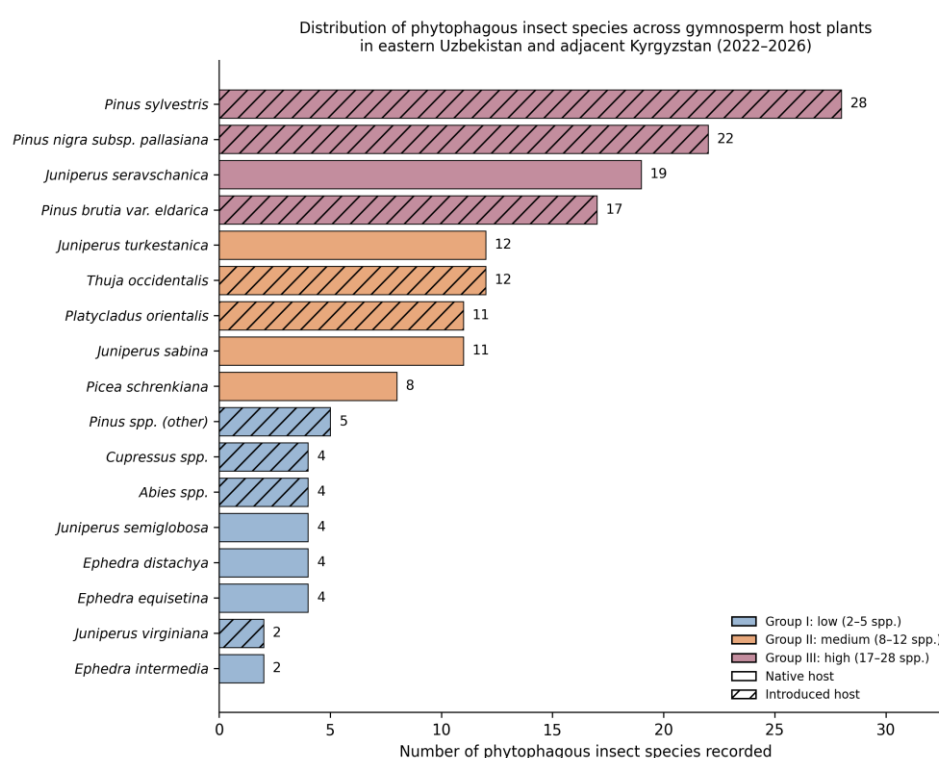


Figure 2. Distribution of phytophagous insect species across 17 native and introduced gymnosperm host plants in eastern Uzbekistan and adjacent Kyrgyzstan (2022–2026). Bars are colour-coded by the diversity group (I, II, III) and hatched for introduced hosts. Counts above each bar indicate the number of phytophagous insect species recorded.

Group I — low diversity (2–5 insect species). This group comprised *Pinus* spp. (5 species; 6.9 % of total entomofauna), *Ephedra equisetina* (4; 5.6 %), *E. distachya* (4; 5.6 %), *Juniperus semiglobosa* (4; 5.6 %), *Abies* spp. (4; 5.6 %), *Cupressus* spp. (4; 5.6 %), *E. intermedia* (2; 2.8 %) and *Juniperus virginiana* (2; 2.8 %). Native xerophytic taxa such as *Ephedra* spp. and *J. semiglobosa* host narrow guilds of

specialised phytophages, whereas the introduced *J. virginiana* and *Cupressus* spp. apparently have not yet accumulated a substantial native insect fauna.

Group II — medium diversity (8–12 insect species). *Picea schrenkiana* (8; 11.1 %), *Juniperus sabina* (11; 15.3 %), *Platycladus orientalis* (11; 15.3 %), *J. turkestanica* (12; 16.7 %) and *Thuja occidentalis* (12; 16.7 %) supported intermediate assemblages in which obligate (primary) and facultative (secondary) phytophages occurred in similar proportions. *P. schrenkiana* hosted specialised bark- and wood-boring insects, while the introduced Cupressaceae *T. occidentalis* and *P. orientalis* appeared to attract broadly polyphagous species from the surrounding landscape.

Group III — high diversity (17–28 insect species). *Pinus sylvestris* (28; 38.9 %), *P. nigra* subsp. *pallasiana* (22; 30.6 %), *Juniperus seravschanica* (19; 26.4 %) and *P. brutia* var. *eldarica* (17; 23.6 %) hosted the richest assemblages. The dominance of introduced *Pinus* species in this group reflects their dense and even-aged urban plantations, which provide a continuous and structurally simplified habitat. *Juniperus seravschanica*, the only native taxon in this group, owes its high richness to its broad geographic range, large biomass and long co-evolutionary history with the regional fauna.

3.2. Ecotopic distribution

Insect assemblages partitioned clearly between ecotopes. Urban ecosystems supported the largest pool of introduced host plants (nine taxa, Figure 2) and the highest representation of adventive insect species, including *Cinara palaestinensis*, *C. pinimaritimae* and *Leptoglossus occidentalis* Heidemann (Coreidae). The *adir* ecotope was characterised by a depauperate *Ephedra*-associated assemblage of small, host-specific Hemiptera and a few oligophagous Coleoptera. Piedmont juniper woodlands harboured the richest native fauna, dominated by Scolytinae and Buprestidae attacking *J. seravschanica* trunks and branches. Mountain forests added

a small set of cool-adapted Lepidoptera and Diprionidae that were rare or absent in the lowlands.

3.3. Adventive species

Three adventive species merit explicit mention. *Cinara palaestinensis* and *C. pinimaritimae* were recorded on ornamental *Pinus brutia* var. *eldarica* and *P. nigra* subsp. *pallasiana* in urban plantings of the Fergana Valley, with identifications confirmed by COI barcoding [17]. *Leptoglossus occidentalis*, an established global invader of *Pinus* cones [18,19], was observed in low numbers on *Pinus sylvestris* and *P. nigra* subsp. *pallasiana* in city parks. The cypress bark beetle *Phloeosinus aubei* (Perris) [20] was repeatedly recorded on *Thuja occidentalis*, *Platycladus orientalis* and *Juniperus virginiana*, indicating that ornamental Cupressaceae act as bridgeheads for this Mediterranean species in Central Asia.

4. Discussion

Our survey provides the first synthetic, host-resolved account of the phytophagous entomofauna of gymnosperms across the ecotopic gradient of eastern Uzbekistan and adjacent Kyrgyzstan. Three patterns deserve particular attention.

Disproportionate richness on introduced *Pinus* species. Although none of the *Pinus* taxa surveyed are native to the study region, they collectively account for the highest number of associated phytophages, with *Pinus sylvestris* alone harbouring 28 species (38.9 % of total). This pattern is consistent with the predictions of plant apparency theory and of recent meta-analyses showing that widespread, structurally simple plantings of introduced conifers accumulate large insect assemblages composed of both native polyphages and accompanying adventive specialists [6,9,21]. In our case the high richness reflects a combination of: (i) extensive even-aged urban plantations that concentrate suitable resources; (ii) the wide native range of *P. sylvestris* in northern Eurasia, which makes its associated fauna easily available for colonisation; and (iii) the arrival of co-introduced specialists such as *Cinara* spp.



[17] and *L. occidentalis* [18].

Native *Juniperus seravschanica* as a regional hotspot. Among native taxa, *J. seravschanica* supported 19 phytophagous species (26.4 % of total), a value comparable to that of the most pest-rich introduced pines. This is unsurprising given its dominance in piedmont and montane forests and its long evolutionary relationship with regional bark- and wood-boring beetles. By contrast, the closely related *J. semiglobosa* and *J. turkestanica* supported markedly fewer species (4 and 12, respectively), suggesting that within the same genus host availability and phenological window strongly modulate the realised insect community.

Adventive species and urban green spaces as invasion bridgeheads. The recovery of *Cinara palaestinensis*, *C. pinimaritimae* and *Leptoglossus occidentalis* from ornamental urban plantings confirms that Central Asia is participating in the global homogenisation of conifer-feeding insect faunas [11,12]. All three species have well-documented histories of human-mediated long-distance dispersal, and their establishment in eastern Uzbekistan is consistent with patterns reported elsewhere in Eurasia where ornamental *Pinus* plantings act as the first interception point [13,18]. The repeated detection of *Phloeosinus aubei* on introduced Cupressaceae is similarly worrying, given the species' demonstrated capacity to expand into temperate climates with susceptible Cupressaceae plantings [20,22].

Ecotopic structuring. The strong association between ecotopes and host-plant identity (Figure 2) implies that phytophagous insect assemblages cannot be understood without explicit reference to the ecotopic context. The *adir* ecotope, with its low and dry *Ephedra* shrublands, supports a small but distinctive community of host-specific Hemiptera, while urban ecotopes are dominated by polyphages and adventive specialists exploiting introduced Pinaceae and Cupressaceae. Piedmont and montane ecotopes, by contrast, retain assemblages with a higher proportion of



native specialists. This gradient parallels patterns of urban-driven ecological filtering documented for scale insects and other conifer pests in temperate cities [12,23].

Several limitations should be acknowledged. First, our sampling effort was unevenly distributed across host species, with the most abundant taxa receiving the largest number of inspections; rare species totals may therefore underestimate true richness. Second, identification of certain microlepidopteran and homopteran groups remains tentative and will benefit from further barcoding [24]. Third, the four-year window of the survey does not capture multi-decadal dynamics such as the slow establishment of bark beetles or seed bugs, which can build up densities long after first detection [10,19]. Despite these caveats, the patterns documented here are robust enough to support biogeographic interpretation and to inform early-warning programmes.

5. Conclusions

This survey delivers the first ecotope-resolved checklist of phytophagous insects associated with native and introduced gymnosperms in eastern Uzbekistan and adjacent Kyrgyzstan. Three operational diversity groups can be recognised, with introduced *Pinus* taxa and the native *Juniperus seravschanica* sustaining the richest assemblages. Urban ecotopes accumulate adventive species at a measurable rate, and ornamental Cupressaceae and Pinaceae are emerging as the principal entry points for alien conifer pests in Central Asia. The data justify the inclusion of urban green-space inventories in regional invasive-species monitoring schemes and provide a quantitative baseline against which future change—whether driven by further introductions, climate warming, or shifting urban planting practices—can be assessed. Targeted DNA barcoding, sentinel plantings of indicator hosts (especially ornamental *Pinus* species), and coordinated cross-border surveys with Kyrgyz colleagues are recommended as the next steps.



Acknowledgments

The author thanks the academic supervisor and colleagues at the Department of Zoology, Fergana State University, for guidance and logistical support during field work, and the staff of regional botanical gardens and city park services for facilitating access to ornamental plantings. The author also acknowledges fruitful discussions with Central Asian entomologists who contributed identification of selected specimens.

Funding

This research received no external funding.

Data Availability Statement

All data supporting the findings of this study are reported within the article. Voucher specimens are deposited in the entomological collection of the Department of Zoology, Fergana State University. DNA barcode sequences of selected adventive species are available from GenBank as indicated in the cited literature.

Conflicts of Interest

The author declares no conflict of interest.

References

1. Adams, R.P. *Junipers of the World: The genus Juniperus*, 4th ed.; Trafford Publishing: Bloomington, IN, USA, 2014.
2. Farjon, A. *A Handbook of the World's Conifers*, 2nd ed.; Brill: Leiden, The Netherlands, 2017.
3. CEPF. Ecosystem Profile: Mountains of Central Asia Biodiversity Hotspot; Critical Ecosystem Partnership Fund: Arlington, VA, USA, 2017.
4. Kayimov, A.K.; Sultanov, R.A.; Botman, E.K. Conifer plantings of Uzbekistan: introduction, ecology and current state. *Vestnik Tashkent State Agrarian University* 2018, 3, 42–49.
5. Eastwood, A.; Lazkov, G.; Newton, A.C. *The Red List of Trees of Central Asia*; Fauna & Flora International: Cambridge, UK, 2009.



6. Connor, E.F.; Faeth, S.H.; Simberloff, D.; Opler, P.A. Taxonomic isolation and the accumulation of herbivorous insects: a comparison of introduced and native trees. *Ecological Entomology* 1980, 5, 205–211.
7. Brändle, M.; Brandl, R. Species richness of insects and mites on trees: expanding Southwood. *Journal of Animal Ecology* 2001, 70, 491–504.
8. Niemelä, P.; Mattson, W.J. Invasion of North American forests by European phytophagous insects. *BioScience* 1996, 46, 741–753.
9. Kenis, M.; Auger-Rozenberg, M.-A.; Roques, A.; Timms, L.; Péré, C.; Cock, M.J.W.; Settele, J.; Augustin, S.; Lopez-Vaamonde, C. Ecological effects of invasive alien insects. *Biological Invasions* 2009, 11, 21–45.
10. Six, D.L.; Wingfield, M.J. The role of phytopathogenicity in bark beetle–fungus symbioses: a challenge to the classic paradigm. *Annual Review of Entomology* 2011, 56, 255–272.
11. Roques, A.; Auger-Rozenberg, M.-A.; Blackburn, T.M.; Garnas, J.; Pyšek, P.; Rabitsch, W.; Richardson, D.M.; Wingfield, M.J.; Liebhold, A.M.; Duncan, R.P. Temporal and interspecific variation in rates of spread for insect species invading Europe during the last 200 years. *Biological Invasions* 2016, 18, 907–920.
12. Frank, S.D. Review of the direct and indirect effects of warming and drought on scale insect pests of forest systems. *Forestry* 2021, 94, 167–180.
13. Sjöman, H.; Östberg, J.; Bühler, O. Diversity and distribution of the urban tree population in ten major Nordic cities. *Urban Forestry & Urban Greening* 2012, 11, 31–39.
14. Khamraev, A.Sh. *Entomofauna of Uzbekistan: Phytophagous Insects of Cultivated and Wild Plants*; Fan: Tashkent, Uzbekistan, 2004 (in Russian).
15. Mirzaliyeva, K.R.; Kholmatov, B.R. Pests of conifers in the urban plantings of the Fergana Valley. *Uzbek Biological Journal* 2019, 4, 18–24.
16. Nowak, A.; Nowak, S.; Nobis, M.; Nobis, A. Vegetation of solid rock faces and fissures of the alpine and subnival zone in the Pamir Alai Mountains (Tajikistan, Middle Asia). *Phytocoenologia* 2014, 44, 81–101.
17. Zokirov, I.; Zokirova, G.; Khusanov, A.; Ganiev, K.; Makhmudov, M. DNA barcoding and morphological data reveal a wider distribution of *Cinara palaestinensis* and *Cinara pinimaritimae* (Homoptera: Lachninae) in Uzbekistan, Central Asia. *Ecologica Montenegrina* 2025, 87, 1–14.



18. Lesieur, V.; Yart, A.; Guilbon, S.; Lorme, P.; Auger-Rozenberg, M.-A.; Roques, A. The invasive *Leptoglossus* seed bug, a threat for commercial seed crops, but for conifer regeneration? *Insect Science* 2014, 21, 105–113.
19. Bates, S.L.; Strong, W.B.; Borden, J.H. Abortion and seed set in lodgepole and white pine conelets following feeding by *Leptoglossus occidentalis* (Heteroptera: Coreidae). *Environmental Entomology* 2002, 31, 1023–1029.
20. Mendel, Z. Biology of *Phloeosinus armatus* and *P. aubei* (Coleoptera: Scolytidae) in relation to mortality of cypress trees in Israel. *Phytoparasitica* 1984, 12, 89–97.
21. Strong, D.R.; Lawton, J.H.; Southwood, T.R.E. *Insects on Plants: Community Patterns and Mechanisms*; Blackwell: Oxford, UK, 1984.
22. Knížek, M.; Beaver, R. Taxonomy and systematics of bark and ambrosia beetles. In *Bark and Wood Boring Insects in Living Trees in Europe*; Lieutier, F. et al., Eds.; Springer: Dordrecht, The Netherlands, 2004; pp. 41–54.
23. Hanks, L.M.; Denno, R.F. Natural enemies and plant water relations influence the distribution of an armored scale insect. *Ecology* 1993, 74, 1081–1091.
24. Hebert, P.D.N.; Ratnasingham, S.; deWaard, J.R. Barcoding animal life: cytochrome c oxidase subunit 1 divergences among closely related species. *Proceedings of the Royal Society B* 2003, 270 (Suppl.), S96–S99.
25. Borowiec, N.; Thaon, M.; Brancaccio, L.; Cailleret, B.; Ris, N.; Vercken, E. Early population dynamics of *Leptoglossus occidentalis* in introduced range and implications for management. *Forest Ecology and Management* 2018, 429, 1–10.