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Original Paper

EFFECTS OF PINE NEEDLE EXTRACTS ON THE LIFESPAN OF FRUIT FLY *DROSOPHILA MELANOGASTER*

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Herbivores exert constant selective pressure, and many plants respond by supplying their leaves with an array of chemical defences. Terpenoids, polyphenols, and resin acids top this list, with proven antimicrobial and insecticidal properties. However, little is known about the long-term effects of these compounds on insect lifespan. In this study, we investigated how dietary supplementation with Scots pine (*Pinus sylvestris*) needle extract affects the longevity of the fruit fly (*Drosophila melanogaster*), which is a standard model species for studying longevity, toxicity, and physiology. We used a standard survival assay to test the effects of fly diet with 1% and 5% (w/v) pine extract mixed in and assessed sex-specific responses. We found a significant reduction in lifespan at both concentrations in both sexes. While the females in the control group significantly outperformed males in mean lifespan, this difference disappeared completely after treatment. At higher concentrations, the average lifespan of the insects dropped by about 35–40%. We propose that the apparent decrease in longevity may be related to the antibacterial properties of resin acids and essential oils. Microbiome impairment can lead to energy imbalance and chronic physiological stress, especially in females, requiring large amounts of energy due to reproductive demands. Our results support the hypothesis that pine needle extracts impair insect fitness and highlight the potential of pine needle extracts as environmentally friendly botanical insecticides.

Key words: survival analysis, insects, botanical insecticides, plant chemical defenses, sex-specific responses.

INTRODUCTION

During their co-evolutionary arms race, plants and herbivores have been shaping each other's traits for millions of years. Specifically, plants have evolved numerous constitutive and inducible defence strategies against herbivores, especially pest insects (Karban and Baldwin, 1997; Agrawal, 1999; Strauss *et al.*, 1999; Dicke & van Loon, 2000; Schoonhoven *et al.*, 2005). Defensive responses of plants against insect feeding or egg deposition induce several bioactive signals from the wounded tissues. These bioactive specialised plant defence compounds may repel or intoxicate insects, affecting their digestive system and microbiome (Fürstenberg-Hägg *et al.*, 2013).

In coniferous trees, the primary defences against insect pests are specialised morphological structures and

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needle and bark chemicals, including terpenoids, phenolics, vitamin C, organic acids, tannins, alkaloids, and essential oils (Franceschi *et al.*, 2005; Novick *et al.*, 2012; Sajid *et al.*, 2018; Klavins *et al.*, 2023). The concentration of these chemicals provides high antioxidant activity in pine needles (Gutiérrez-del-Río *et al.*, 2021). The higher the antioxidant level, the greater the antibacterial and antifungal activity (Ispiryan *et al.*, 2024), which explains why pine needles can be used to produce chemicals for antiseptic, antimicrobial, and antifungal protection. Because of their high chemical activity and antioxidant properties, pine needle extracts can be used to prepare botanical pesticides (Gutiérrez-del-Río *et al.*, 2021). These compounds act on insects by repelling, deterring feeding and oviposition, and interfering with physiological activities (Isman, 2014; Laxmishree and Nandita, 2017). Terpenoids and phenolics are especially well-known for their pest-repellent functions (Bell and Rarestad, 1987; Ansari *et al.*, 2005). As plant antioxidants, polyphenols have various pharmacological and therapeutic properties, including anticancer, anti-inflammatory, antioxidant, and vascular protective properties (Zhang *et al.*, 2022). Some conifer species have even been established as reference systems for information on anatomical, chemical, biochemical, molecular, and genomic aspects of conifer chemical defences (Zulak and Bohlmann, 2010). However, while conifer chemical defences provide a strong and durable shield of protection against most generalist herbivores and non-pathogenic fungi, this protection is not ubiquitous, as some insect pests thrive under plant defensive reactions, or their development, reproduction, and lifespan are impaired relatively little (Bohlmann, 2012).

The effects of pine-derived bioactive chemicals on insect pests are well known. The needles also contain resin acids, which play an important role in defence against infections and parasites (Bhardwaj *et al.*, 2021). The essential oils of pine are used in common practice as insect repellents and have toxic effects on pests (Ansari *et al.*, 2005; Bohlmann, 2012). A likely mechanism of action could be the high concentration of monoterpenes (Bell and Rarestad, 1987), which effectively inhibit the growth of bacteria, including microbial symbionts in the insect digestive tract (Kim and Shin, 2005; Trapp and Croteau, 2001). Such effects can be considered universal, seriously affecting the fitness of an organism. Nevertheless, it is not obvious how frequent ingestion of bioactive substances in the diet of insects might affect their lifespan.

In this study, we investigated how Scots pine (*Pinus sylvestris*) needle extract affects fruit fly (*Drosophila melanogaster*) lifespan, and we also considered the role sex differences may play in differentially influencing fly lifespan. We predicted a decrease in insect lifespan with increasing concentrations of pine needle extract in their diet. This species has been selected as a frequently used model organism for studies of longevity, toxicity, and mortality (Piper and Partridge, 2018; Ogienko *et al.*, 2022). In addition, a closely related species of *D. melanogaster*, *D. suzukii*, is a significant invasive pest of soft-skinned fruit, especially ripening berry crops (Toxopeus *et al.*, 2016; Cai *et al.*, 2019; Renkema *et al.*, 2022). Pine needle extract was selected as an active component since it is a local resource from which biopesticides can be produced (Klavins *et al.*, 2023).

MATERIALS AND METHODS

Fruit flies

For this study, Oregon-R-modENCODE(#25211) wild strain obtained from the Bloomington Drosophila Stock Center (Indiana University, Bloomington, IN, USA) were used. Fruit flies were kept at a constant temperature of 25 ± 1 °C and at a humidity of about 50%. A day-night cycle of 12:12 hours (h) was maintained. A standard diet was used, based on a recipe adapted from Cold Spring Harbor Protocols (Lewis, 1960). Tegosept (methyl-p-hydroxybenzoate, Genesee Scientific) at a concentration of 10% was used as an antifungal agent.

Lifespan experiment

To obtain synchronised eggs, a paste of live yeast (6 millilitres (ml) of water mixed with 3 grams (g) of dry live yeast) was prepared to stimulate egg laying. The paste was placed on a Petri dish with grape juice jelly (1.5 g agar per 100 ml juice). For egg laying, 100 pairs of *Drosophila* were released into the cage with the Petri dish for 24 h. The eggs were then transferred to vials with the standard diet for subsequent development. The diet medium was prepared by adapting a Cold Spring Harbor Protocol. Specifically, 100 ml of water was combined with 4 g dextrose, 7 g cornmeal, 0.9 g agar, and 2 g of deactivated yeast. To prevent fungal contamination, a 10% Tegosept stock solution (methyl-p-hydroxybenzoate; Genesee Scientific) was added into the mixture. The medium was dispensed into tubes at approximately 9 g per vial.

Adult flies usually start to hatch on day 9. We considered this to be fast development and discarded these *Drosophila* to control for phenotypic variation linked to developmental time. In this way, selection for early emergers was prevented. Day 10 is a normal pace of development, so only these flies were used for observations of lifespan. Collecting flies with normal developmental speed also allows to obtain the maximum number of synchronised individuals.

All flies were briefly anaesthetised once with carbon dioxide (CO_2) for distribution into vials. Ten flies of the

same sex were placed in each vial, ten vials per group ($n_1 = n_2 = n_3 = 100$ individual flies per group). Flies were transferred to vials with fresh food without the use of anaesthesia every three days. For the trial groups, pine needle extract at concentrations of 1% and 5% weight per volume (w/v) was added to the standard diet. The extract was added during the course of feed preparation, when the mixture cooled slightly but was still fluid (i.e. approximately 50–55 °C).

Pine needle extract components

Pine needles contain a large number of compounds, which can be divided into two large groups according to the method of their extraction. The most prominent components are those that are soluble in low-polarity solvents: essential oils, carotenoids, lipid vitamins (A, E, K, D), resin acids, alcohol derivatives, polyprenols (Rogachev and Salakhutdinov, 2015) and waxes (Attard *et al.*, 2018).

Water-soluble components are also found in the needle composition: vitamins (Horn and Chapman, 2014), polyphenols (Metsämuuronen and Siren, 2014), carbohydrates (Duquesnoy *et al.*, 2008), and shikimic acids (Bochkov *et al.*, 2012).

The extract itself was obtained from *Pinus sylvestris* green biomass by a biorefinery process following the method described by Roshchin *et al.* (1994).

Statistical analyses

The Kaplan-Meier approach was used to estimate lifespan (Kaplan and Meier, 1958). Mean survival time was estimated as the area under the survival curve. This indicator is based on the entire range of data. Irwin's restricted mean lifespan was also included. Vials in which flies escaped or died accidentally were excluded from the survival analysis.

In this study, we emphasise early deaths, so the Fisher's exact test was used to facilitate comparisons of mortality at different time points. The nearest observed day that a certain percentage mortality passed was used.

All computations were performed in Oasis 2 software (Han *et al.*, 2016).

RESULTS

Lifespan

We found significant differences in male and female lifespan between the control group and each of the two groups with different concentrations of pine extract and between the two treatment groups as well (Fig. 1A, 1B). Greater concentration of pine extract was correlated to decreased survival rates.

Mean lifespan

The control groups of male and female flies had the highest mean lifespan — 50.74 and 62.68 days, respectively. The mean lifespans of the male groups living on diets supplemented with pine extract at 1% and 5% w/v concentrations were 42.8 and 32.66 days, respectively. The mean lifespans of the female groups living on diets supplemented with pine extract at 1% and 5% w/v concentrations were 43.21 and 34.75 days, respectively (Table 1). The differences between all male and all female groups at all time points were statistically significant (Table 2).

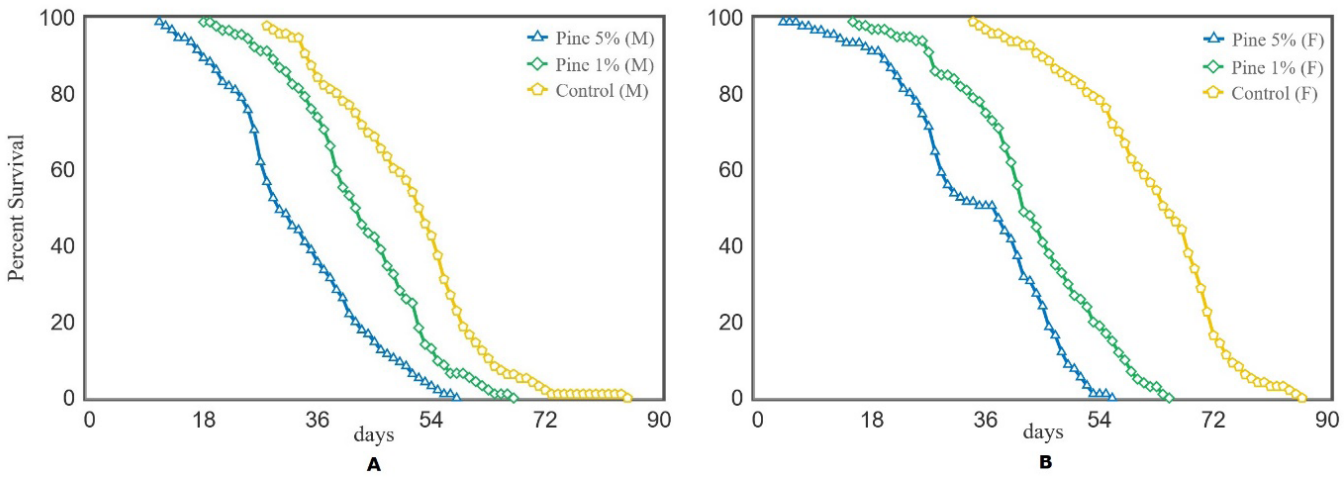


Fig. 1. Mortality plot of *Drosophila melanogaster* males (A) and females (B) living on a standard diet (control group, pentagons) and on a diet supplemented with pine extract at concentrations of 1% (diamonds) and 5% (triangles) w/v. Differences between all groups are statistically significant ($p < 0.05$).

Table 1. Mean and median values of lifespan of different groups of males (M) and females (F) at different life intervals. SE, standard error; CI, confidence interval

Condition	*n* of subjects	Restricted mean, days	Restricted mean, SE	Restricted mean, 95% CI	Linear interpolation of mortality curve, 25%	Linear interpolation of mortality curve, 50%	Linear interpolation of mortality curve, 75%	Linear interpolation of mortality curve, 90%	Linear interpolation of mortality curve, 100%
Pine 5% (M)	95	32.66	1.14	30.43 ~ 34.90	25.15	29.83	40.31	49.5	58
Pine 1% (M)	92	42.8	1.1	40.66 ~ 44.95	35.5	42	51	54.93	67
Control (M)	96	50.74	1.15	48.48 ~ 53.00	42	52	57.5	63.2	85
Pine 5% (F)	91	34.75	1.26	32.28 ~ 37.22	25.92	37.17	44.75	48.63	56
Pine 1% (F)	100	43.21	1.13	40.99 ~ 45.43	36	41.86	51.5	58	65
Control (F)	97	62.68	1.19	60.35 ~ 65.01	55.31	64.25	70.63	74.65	86

Table 2. Comparison of all male (M) and all female (F) groups at multiple time points. All differences are considered significant at $p < 0.05$

Condition	*p* at 25%	*p* at 50%	*p* at 75%	*p* at 90%
Pine 5% (M) vs Pine 1% (M)	5.10E-08	0.0000024	0.0002	0.0221
Pine 5% (M) vs Control (M)	3.10E-13	1.40E-12	1.30E-11	0.0000032
Pine 1% (M) vs Control (M)	0.0211	0.0001	0.000007	0.024
Pine 5% (F) vs Pine 1% (F)	0.0001	0.0135	0.0006	0.0001
Pine 5% (F) vs Control (F)	1.20E-12	7.10E-13	9.10E-13	0.000017
Pine 1% (F) vs Control (F)	3.40E-10	1.10E-12	2.50E-13	0.000006

DISCUSSION

In this study, we collected the data on the lifespan of *D. melanogaster* of different sexes subjected to a diet supplemented with pine (*Pinus sylvestris*) needle extract. Our results indirectly confirm the observations of previous researchers. We found that saturating the diet of flies with this extract dramatically reduced their lifespan, regardless of sex (Fig. 1A, 1B). We attribute these effects to the action of certain pine needle compounds. We suggest this is primarily the toxic effect of resin acids, which are known as the defence mechanism of trees against parasites and for their antibacterial properties (Rogachev and Salakhutdinov, 2015; Bhardwaj *et al.*, 2021). Also, it has long been known that the essential oils in the needles have strong antimicrobial properties (Himejima *et al.*, 1992). Essential oil components exhibit antioxidant activity in the scavenging for free radicals and lipid peroxidation (Kwak *et al.*, 2006; Sokół-Łętowska *et al.*, 2007). Further studies showed that the bactericidal mechanism lies in the induction of cytoplasmic outflow and plasmolysis (Zeng *et al.*, 2012). In these studies, extracts have been successfully used to inhibit many food-borne microorganisms, most notably gram-positive bacteria (Metsämuuronen and Siren, 2014; Wedagama *et al.*, 2021).

Pine needles include a large number of components that are generally regarded as health-improving substances, for example, vitamins C, A, E, K and D, alkaloids that prevent degenerative diseases (Singh *et al.*, 2022), shikimic acid used to treat Influenza A and B (Ozhimkova *et al.*, 2019), anti-inflammatory polyphenols commonly used in pharmaceuticals (Dziedziński *et al.*, 2020; Lučinskaitė *et al.*, 2021), and many other phytoactive compounds. It is also important to mention that all these components are easily extracted by simple infusion in hot water and therefore have long been successfully used in traditional medicine to combat seasonal illnesses and scurvy (Schick, 1943; Raal *et al.*, 2018). However, these effects seem to apply to humans and other vertebrates, while insects like *D. melanogaster* incur fitness costs when fed with phytochemical compounds of pine needle extracts. This shows that extract from pine needles may have application not only as a repellent, as has been shown in many studies (Thorsell *et al.*, 1998; Ansari *et al.*, 2005; Maia and Moore, 2011), but also as a mild natural insecticide that reduces insect longevity.

In our study, control groups of fruit flies living on a standard diet demonstrated significant differences in lifespan (Fig. 2A) — females lived about 12 days longer on average (Table 1). Supplementing a small amount of the extract sharply reduced longevity regardless of sex (Fig. 2B), and intriguingly, mean lifespan of males and females became equal and females were unable to maintain the advantage observed in the control group. It can be speculated that females are more susceptible to phytotoxic effects from the pine extract, nevertheless, further increasing the concentration of the extract did not lead to even more significant effects (Fig. 2C), as

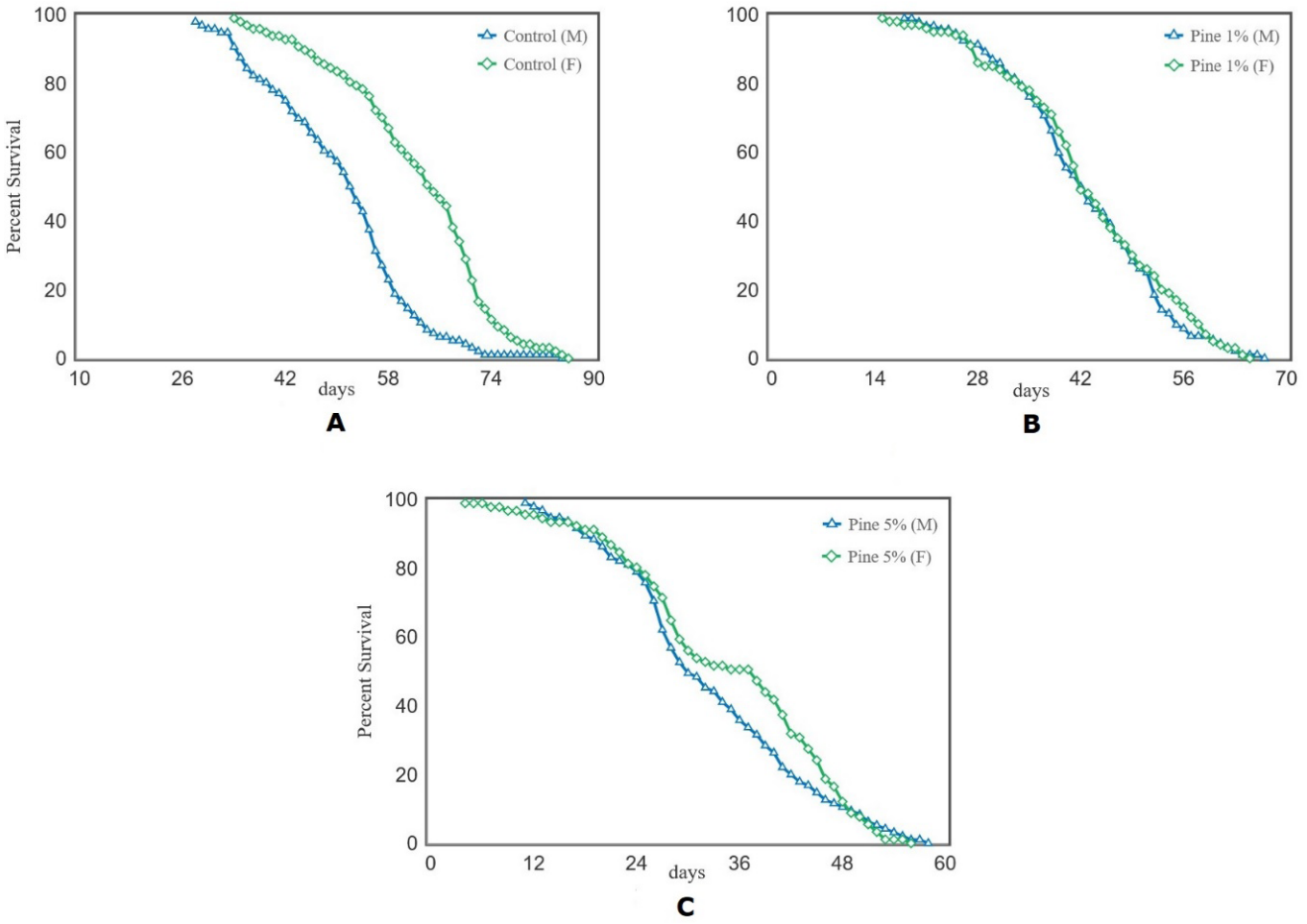


Fig. 2. Comparisons of mortality plots of male (triangles) and female (diamonds) *Drosophila melanogaster* living on different diets. (A) A mortality plot of male and female Control groups. Difference is statistically significant ($p < 0.05$). (B) A mortality plot of male and female groups subjected to a diet supplemented with pine extract at concentration of 1% w/v. Difference is not significant ($p = 0.61$). (C) A mortality plot of male and female groups subjected to a diet supplemented with pine extract at concentration of 5% w/v. Difference is not significant ($p = 0.29$).

the mean life expectancy of *Drosophila* fell identically, irrespective of sex.

We attribute this peculiarity to several interrelated factors. The first relies on the characteristic of pine needle essential oils to suppress the microbiome. This can lead to the organism receiving an insufficient amount of energy. For females, constant quality access to energy is of critical importance, as they expend a significant resource on egg development. We also believe that the natural and easiest way to compensate for this deficiency is simply through eating more. Increasing the duration and frequency of food intake may come at the expense of reduced sleep time. Disruptions in circadian rhythms lead to chronic stress; in insects these are changes in the functioning of the prothoracic gland, which controls the cyclic release of ecdysteroids (Di Cara and King-Jones, 2016). Chronic stress is also known to reduce insulin sensitivity, which amplifies the lack of energy due to a suppressed microbiome and further affects the expected lifespan of females (Krama *et al.*, 2023; Popovs *et al.*, 2024).

This study shows that the repellent properties of conifers are not only determined by their direct toxicity to insects. We can observe a link between behaviour and physiology, and the way chronic environmental stress can translate into metabolic disorders. This is an intriguing area for further research, as the use of natural products as biopesticides and repellents is becoming increasingly relevant and in demand, yet our knowledge of underlying mechanisms is not particularly diverse. Future research should examine the effects of different substances in pine needle extracts to disentangle their effects on insect lifespans. This could help find novel compounds to repel insects and control their populations.

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PRIEŽU SKUJU EKSTRAKTU IETEKME UZ AUGĻU MUŠU *DROSOPHILA MELANOGASTER* DZĪVES ILGUMU

Augēdāji rada pastāvīgu ietekmi uz augiem, un daudzas augu sugas reaģē uz kukaiņiem augēdājiem, sintezējot lapās dažādus ķīmiskās aizsardzības savienojumus. Terpenoīdi, polifenoli un sveķos esošās skābes ir svarīgākie augu aizsardzības līdzekļi, kuriem piemīt antimikrobiālas un insekticīdas īpašības. Tomēr pētījumu par šo vielu ietekmi uz kukaiņu dzīves ilgumu ir maz. Šajā pētījumā augļu mušu (*Drosophila melanogaster*) barībai tika pievienots parastās priedes (*Pinus sylvestris*) skuju ekstrakts, lai noskaidrotu, kā tas ietekmē mušu dzīves ilgumu. Augļu mušas ir viens no dzīves ilguma, toksikoloģijas un fizioloģijas pētījumu modeļorganismiem. Ar standarta izdzīvošanas testa palīdzību tika pētīta barības, kuras sastāvā bija priežu skuju ekstrakts 1% un 5% koncentrācijā, ietekme uz mušu dzīves ilgumu un ar dzimumiem saistītās reakcijas. Tika konstatēta nozīmīga dzīves ilguma samazināšanās abu dzimumu un ekstrakta koncentrāciju grupās. Kontrolgrupās mātītes caurmērā dzīvoja ilgāk par tēviņiem, bet eksperimentālajās grupās mātīšu un tēviņu dzīves ilgums neatšķīrās. Augļu mušām, kuru barībai tika piejaukts priežu skuju ekstrakts 5% koncentrācijā, dzīves ilgums samazinājās par 35–40%. Šādu būtisku dzīves ilguma samazināšanos var skaidrot ar priežu skujās esošo vielu antimikrobiālo ietekmi. Mikrobioma funkcionēšanas traucējumi var ietekmēt enerģijas apmaiņas procesus un radīt hronisku fizioloģisku stresu, kas varētu būt īpaši būtiski mātītēm, kurām vairošanās procesā ir nepieciešami ievērojami enerģijas resursi. Šī pētījuma rezultāti atbalsta hipotēzi par priežu skuju produktu negatīvo ietekmi uz kukaiņu bioloģisko fitnesu, kā arī pasvītro priežu skuju ekstraktu, kā videi draudzīgu augu izcelsmes insekticīdu, potenciālu.