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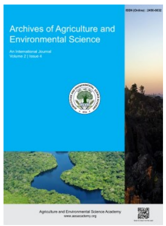

ORIGINAL RESEARCH ARTICLE

Biophysical and temporal factors influenced population dynamics of woolly aphid, codling moth and mealybug in apple (*Malus domestica* B.) production of southern Ethiopia

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ABSTRACT

Apple is one of the most popular fruit crops globally, including Ethiopia. However, its productivity is adversely influenced by many constraints. Insect pests, such as woolly apple aphids, codling moths, and mealybugs, are major damaging biotic constraints globally, including Ethiopia, and their population dynamics are significantly influenced by biophysical and temporal changes. Field surveys were conducted in the Chencha highlands of southern Ethiopia during the 2021 and 2022 main rainy and off seasons to determine the prevalence and incidence of these insect pests and the associations of biophysical and temporal factors with these pests' population changes. Multistage random sampling approaches were followed for data collection, and consequently, 164 apple fields were inspected for insects' occurrence. Logistic regression analyses were employed to determine the association of independent variables with the incidence of each insect pest. Results showed that the prevalence (90.18, 75.61, and 50.45% in 2021 and 70.26, 54.15 and 36.48% in 2022, respectively), incidence, and number of individual insects per tree varied across years, seasons, and other biophysical factors. These parameters were higher in the off-season in 2021 than in the main rainy season in 2022. Accordingly, incidences of aphids, codling moths, and mealybugs were recorded at about 57.56, 54.93, and 33.29% in 2021, and 37.01, 40.78%, and 21.23% in 2022, respectively. Association analyses revealed that independent variables such as years, seasons, altitude, age of tree, growth stages, cropping systems, weed infestation, and tree management were significantly (*P*<0.001) associated with the incidences of all studied insects in the reduced multiple regression model. Apple cultivation at an altitude of ≤2500 m and main rainy season with recently planted trees (≤5 years), flowering to fruit development growth stages, high weed infestation, and tree management through composting and pruning had significant associations with low wooly aphids (≤15%), codling moths (≤40%), and mealybug (≤20%) incidence and can be considered as management options to reduce the aforementioned insects and associated yield losses to ensure apple production.

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INTRODUCTION

Apple (*Malu sdomestica* Borkh.) is one of the most widely grown fruit crops worldwide, growing main in temperate regions of the globe (FAO, 2023). Apple ranks fourth in terms of global fruit production. Around 83.74 million metric tons of apples are produced worldwide. It accounts for 50% of the world's deciduous fruit tree production. China is the leading apple-growing country, producing about 40.82 million tons, followed by the European Union (11.07 tons), the United States (4.56 tons), Turkey (4.40 tons), and India (2.19 tons) (USDA, 2024). South Africa is Africa's top producer, followed by Egypt, Kenya and

Morocco (FAO, 2023). British protestant missionaries brought the fruit to Ethiopia in 1950, mainly to the Chencha district, where it was planted at the Kale-Hiwot church garden (Girmay *et al.*, 2014). The zone agricultural office reports that in the Gamo zone, apple fruits covered approximately 7123.40 hectares in 2022/23 and produced 142,468 tons overall. This was slightly more than the previous (2021/22) growing season's coverage of 5938.8 hectares and 118538.45 tons. From the earliest introduced areas of Chencha district to most of the highland areas of the country, apple output has been steadily rising. Accordingly, apple fruit is produced widely in highland areas of the south, Oromia, Amhara, and Tigray regions of the country (Mola, 2018). To date, there is increased demand and consideration in apple and other highland fruit production in most highlands of areas of the country as commodities and income generation that can provide opportunities for livelihood welfare and developments. However, with the increasing demand for apple fruit in Ethiopia, it relies on imports from abroad, such as France, South Africa, and the United States, which account for about 39.2%, 23.7%, and 12.8% in that order (Tamirat & Muluken, 2018).

Apple cultivation is by far one of the most significant agricultural practices that make a vital environmental, social (Admasu *et al.*, 2022), and nutritional (Ferretti *et al.*, 2014) contribution for millions of the global population. Moreover, it plays a significant role in the economies of developed and many developing countries in the world (USDA, 2022). Apple fruit is an essential food that is major nutritional sources of vitamins (C, K, and B6), minerals (Ca, P, K, Fe, and Mg), carbohydrates, proteins, and fibers (Adyanthaya *et al.*, 2010; Ferretti *et al.*, 2014). The crop provides a means of livelihood for small-scale cultivators and exporters, bearing noteworthy consequences for the nation's foreign exchange earnings (Girmay *et al.*, 2014; Alemu, 2020). Interestingly, there is evidence that apple plantations mitigate current climate change scenarios (Admasu *et al.*, 2022). Previous reports also indicated that through reducing soil and water erosion and sequestering carbon, apples have a direct impact on environmental pollution (Admasu & Jenberu, 2022; Beyene *et al.*, 2022; Hardie *et al.*, 2024). Additionally, it is socioeconomically significant since it gives rural communities' women and youth job opportunities (Girmay *et al.*, 2014; Alemu, 2020).

Despite its many advantages, biotic challenges (like diseases, insect pests, and weeds), abiotic stress (climate changes, soil fertility, irrigation water access at critical periods, etc.), socioeconomic conditions (like availability of improved apple production technologies, land use management, etc.), and poor field management practices limit its production and productivity in Ethiopia (Girmay *et al.*, 2014; Beyene *et al.*, 2022). Of the biotic restraints, woolly apple aphids [*Eriosoma lanigerum* Hausmann (Hemiptera: Aphididae)] (Beers *et al.*, 2010; Vashisth *et al.*, 2024), codling moths [*Cydia pomonella* Linnaeus (Lepidoptera: Tortricidae)] (Zhao *et al.*, 2015; Etienne *et al.*, 2024), and apple mealybugs [*Phenacoccus aceris* Signoret (Homoptera: Pseudococcidae)] (García-Álvarez *et al.*, 2014; Sá & Oliveira, 2021) are among those significantly influencing and destructive insect pests of apple production in the producing countries of the world. However, the latter two insect pests were not reported in Ethiopia, despite being regularly observed and their economic significance being well known by extension specialists in the zonal and district agricultural offices in the country's apple-producing regions. The woolly apple aphid was previously reported in Ethiopia (Girmay *et al.*, 2014; Mola, 2018).

Woolly apple aphids are known for sucking insects and forming densely packed colonies enclosed with white, waxy, filamentous secretions on the above-ground parts and on the roots of apple trees (Shaw & Walker, 1996). Crawlers (first instar nymphs) are produced mainly by overwintering females that reproduce at a relatively slow rate below ground, on the roots of the tree (Damavandian & Pringle, 2007; Gresham, 2013), and dispersal is primarily through the crawlers movements (Mols & Boers, 2001; Lordan *et al.*, 2015). Dry climates and cool environments are favourable conditions for fast reproduction and dispersal, and their population changes are significantly influenced by such phenomena (Heunis & Pringle, 2006; Gresham, 2013). Favourite feeding sites for woolly apple aphids are pruning and wound areas, branches, leaf axils, new growth shoots, and the roots (Mueller *et al.*, 1992). Their feeding activity causes galls to form on the woody tissue, which can lead to the destruction of young lateral shoots and buds (Heunis & Pringle, 2006). Above-ground damage by woolly apple aphid includes the destruction of developing buds in the leaf axils and a reduction in tree vigour due to aphid feeding in leaf axils (Pringle & Heunis, 2001; Heunis & Pringle, 2006). Depending on varietal susceptibility and environmental factors, it can cause a yield loss of 2.4 kg per tree if fields are left unmanaged (Brown *et al.*, 1995).

Codling moth is an insidious pest, tunneling/burrowing to the core of valuable commodities (like apple fruit) that are typically marketed with exceptional quality standards for appearance, firmness, and sweetness. The codling moth overwinters as a full-grown caterpillar within a cocoon, pupating in winter or early spring (Mangan, 2016). The ideal temperature range for moth development and hatching is 16.6 °C to 25 °C. Adult moths emerge in the spring and deposit their eggs directly on apples and leaves. Codling moth feeds inners of apple fruits, which makes the fruit unsuitable for consumption, i.e., the larvae tunnel towards the apple cores and feed on the seeds before exiting the fruit (Mangan, 2016). Because of this, if left uncontrolled, it can result in exceptionally high levels of damage, up to 90% of the fruit crop (Anderson *et al.*, 2013; Mangan, 2016). On the other hand, apple mealybugs are sucking insects with oval soft bodies and rose to whitish color, with their bodies covered by a white waxy substance similar to powdery or floury cotton; they have a pair of waxy filaments around the top of their bodies (Silva *et al.*, 2016). Because of their univoltine nature, apple mealybugs overwinter as second instar nymphs inside a white cocoon embedded in the tree bark, in crevices. They emerge from their overwintering spot in the early spring. On sunny days, the nymphs become active, move around, and attach to start feeding. Dispersal is mainly through nymphs to nearby plant tissues. When the fruits are covered in sooty molds due to the pest's secretion of honeydew, there is significant damage upon harvest. Moreover, it can also directly infest and feed on fruit and cause the fruit unsuitable for harvesting and consumption (Bangels *et al.*, 2011).

Despite the importance of the insect pests and their potential to cause significant crop damage and yield losses in apples in the study areas and country as a whole, few survey works (particularly woolly apple aphids, not for others) have been conducted on the distribution and impacts on crop rather than studying what factors influence their occurrence and expansion in Ethiopia (Fetena & Lemma, 2014; Kebede, 2015; Woto & Aloto, 2023). However, agronomic practices, cropping systems, production seasons, and environmental conditions can all have an impact on the occurrence of insect pests, the spread of epidemics, population dynamics, the extent of crop damage, and the resulting yield loss. In this connection, Mengesha *et al.* (2021) and Etienne *et al.* (2024) reported that inspecting the impact of diversified agronomic practices, cropping systems, and environmental factors on insect pest occurrence and crop production is important to getting insight on the status and population dynamics of insects. Prevalence, intensity, and relative importance of major insect pests of apples may vary across geographical areas, agronomic practices, cropping systems, over cropping years and seasons, and other biophysical factors. Hence, insect pest monitoring in crop cultivation fields would help in identifying the most important factors that influence the occurrence, spade development, and population dynamics and in designing and developing efficient, environmentally friendly and sustainable management strategies and tactics for the target pests. But detailed understanding of the present status of woolly apple aphids, codling moths, and apple mealybugs and biophysical and temporal factors associated with their expansion, incidence, and population dynamics in the study areas (Chencha district) in particular and country as a general is lacking.

Therefore, the information from this study is useful in developing efficient management options. Survey data are also useful to gain insight into the occurrence, distribution, and population dynamics of woolly apple aphids, codling moths, and apple mealybugs and design knowledge-based insect pest management approaches. Mengesha *et al.* (2021) and Etienne *et al.* (2024) suggested that understanding the association of incidents of insect pests with biophysical and temporal factors is the cornerstone of agro-ecological crop protection that limits the use of pesticides and would help to identify important factors and focus efforts in formulating sustainable management crop packages. Moreover, such information is of paramount significance as it can be associated with crop damage, yield losses, the economic importance of the insects, and the determination of empirical investigation targeting eco-friendly, cost-effective, and affordable management options. Therefore, the present study was initiated with the objectives to determine (i) prevalence, incidence, and relative importance of woolly apple aphids, codling moths, and apple mealybugs in potential apple-producing areas of Chencha highlands in the Gamo zone of southern Ethiopia and (ii) association of the incidences of these insect pests with biophysical and temporal factors that affect their occurrences and population dynamics in the study areas.

MATERIALS AND METHODS

Overviews of surveyed district

Surveys of major apple insect pests, cropping systems, field management practices, and other relevant factors were conducted in selected farmer associations (FAs) in Chencha Highland, southern Ethiopia, during the 2021 and 2022 off seasons (January and February) and main rainy times (July and August). Farmer associations were purposively selected based on apple production potential and the importance of insect pests. Chencha district is located between 06°8' 55'' N to 06° 25'30'' S latitude and 037°29' 57'' E to 037°39'36'' W longitude, with elevations ranging from 1300–3950 meters above sea level (m a.s.l.). According to the Bureau of Agricultural Office in the district, the area exhibits diversified agro-ecologies, in which 18 and 82% of the area are covered with lowland and mid-to extreme-highland, respectively. The area is also characterized by a bimodal precipitation pattern, where the short rainy season falls from March to May and the main rainy season falls from July to November. The area's mean annual total precipitation, temperature, and relative humidity for the last decade were 1170.24 mm, 18.73 °C, and 67.30%, respectively. Weather information for the study area during the 2021 and 2022 production years is presented in Figure 1. In the study areas, the dominant features of the soil's physical and chemical properties are moderate to strongly acidic, with low to moderate organic matter contents ranging from 0.20 to 3.22% and a sandy-loam texture. Crop-livestock mixed farming systems and production of cereals, pulses, root and tubers, vegetables, other fruits, and timber plants are well experienced in the district.

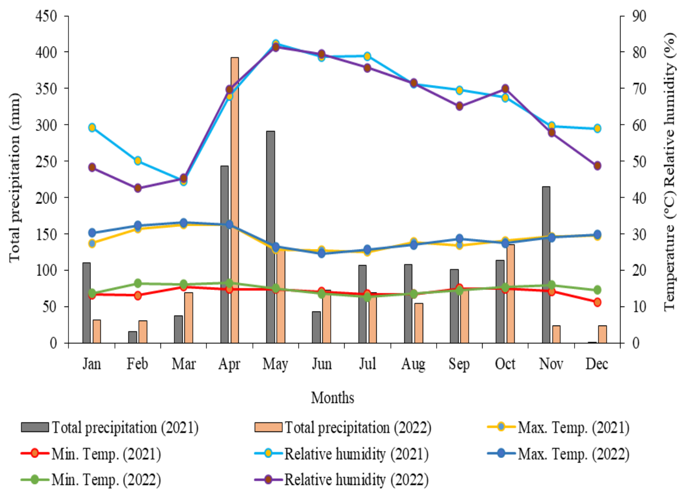

Figure 1. Total precipitation, maximum and minimum temperatures and relative humidity in the Chencha district, southern Ethiopia, during the 2021 and 2022 cropping years.

Survey procedure and sampling units

A multistage random sampling approach was employed with slight adjustments to the procedure. Adjustments were made to target only FAs within the district highly affected by woolly aphids, codling moths, and mealybugs. During the study, the FAs within the district were purposefully selected, but the households for apple field inspection were randomly selected, and in the FAs, the fields with or without the listed insect pests were randomly nominated for the assessment. Similarly, the respondents who cultivated apples were designated using a simple random sampling approach and separately interviewed for data collection. Formal survey questionnaires with structured and semi-structured forms were prepared to collect the necessary information from apple-producing farmers via personal interviews and direct field inspection. Accordingly, four FAs and one private farm were selected based on their production potential for the crop in consultation with the extension expert of the district agricultural office. Fourteen plus one fields per FA and private farm per year, along with an apple grower, were surveyed. Thus, a total of 164 apple fields were assessed across FAs, seasons, and years, of which 82 were assessed for each of the 2021 and 2022 years.

Apple fields were assessed for aphids (*Eriosoma lanigerum*), codling moth (*Cydia pomonella*), and mealybug (*Phenacoccus aceris*) prevalence, incidence, number of individual insects per tree (NIPP), and other relevant information using the developed questionnaires. The questionnaires were primarily focused on information concerning cropping systems, field husbandry practices, and other relevant questions. The primary data were gathered directly from apple fields, whereas secondary data were compiled from the corresponding district's agricultural office, FAs, and the national meteorology agency of the Hawassa branch (Figure 1). The incidence and number of insect individuals per tree of the three insect pests were recorded from 10 randomly selected apple trees by moving diagonal and/or X-fashion transects, depending on the farm size, 100–250 and >250 m^2 in that order. All apple trees in each field were considered sampling units for aphids, codling moth, and mealybug incidence, as well as the number of inset individuals per tree valuation for field size of 100–250 m^2. Samples for each insect pest were taken from each apple field and tree and packed individually in sterile paper bags, labelled, and brought to the Arba Minch Crop Protection Clinic to identify and confirm the target insects.

Woolly aphid, codling moth, mealybug and biophysical factors assessment

Insect pest prevalence, incidence, and NIPP were assessed to determine the distribution, relative importance, and associations of woolly aphids, codling moths, and mealybugs in the study areas over cropping seasons and years. On-site field visits were made at each selected FA as well as farms, and each field was assessed for insect prevalence, incidence, and number of insect individuals per tree. For each insect pest, the prevalence was determined as the ratio of infested apple fields over the total number of fields assessed in each sampled FA, as follows:

$$\text{Prevalence}\ (\%) = \frac{\text{Number of fields with insect pest per farmer association}}{\text{Total number of field assessed per farmer association}} \times 100$$

The incidence of woolly aphids, codling moths, and mealybugs was determined by counting the number of infested trees and expressed as a percentage of the total number of trees regarded per field, as in the following formula:

$$\text{Incidence}\ (\%) = \frac{\text{Number of trees infested with insect pest per field}}{\text{Total number of trees assessed per field}} \times 100$$

Likewise, the NIPP was counted by visual observation on the randomly selected apple trees and averaged to get the mean number for each insect for data analysis. Apart from insect pests assessment, cropping systems and field husbandry practices, which are representing both biotic and abiotic factors associated with apple production, including cropping years (2021 or 2022), seasons (off season or main-rainy season), sources of plant materials (Bureau of Agriculture or Non-government), Field size (< 250 m^2or >250 m^2), planting density (<8 or >8 plants in 100 m^2), altitudinal ranges (<2500 or ≥2500 m a.s.l.), age of tree (<5, 5 to 10, 11 to 15, and >15 years), survey site (farmer field or private farm), growth stages (flowering, fruit development, or fruit maturity), cropping systems (sole, or intercropping with various crops), tree management, and weeding infection (low, intermediate, or high levels) were recorded for each field considered in the survey periods.

Data analyses

Descriptive analysis was performed to describe the distribution, incidence, and NIPP across study areas, years, and production seasons. Woolly aphid, codling moth, and mealybug incidences were used for the association study and classified into distinct groups of binomial qualitative data following Yuen (2006) and Mengesha *et al.* (2021). Categorization of variables and independent variables by contingency tables of the incidences of studied insect pests were built to represent the bivariate distribution of apple fields according to data classifications (Table 1). Class boundaries and cut points for incidence were established based on the mean value of the study variables to all of the inspected fields. Accordingly, class boundaries of <15 and >15%, <40 and >40%, and <20 and >20% were chosen so that binary variable classes were set for incidence of woolly aphids, codling moths, and mealybugs. The association of mean incidence of each insect species with biophysical and temporal factors was analyzed using a logistic regression model (Yuen, 2006) using the SAS procedure of GENMOD (SAS, 2009). The importance of the independent variables was evaluated twice in terms of their effect on the studied insect pest incidences. Initially, a single-variable model was used to assess the relationship between incidence and each independent variable. Subsequently, the association of an independent variable with incidence was tested when entered first and last with all the other variables in the multiple variable model. Independent variables with a significant association with each of woolly aphid, codling moth, and mealybug incidence were consecutively added to a reduced multiple-variable model to determine the significance or risk factor levels of individual variable classes (Yuen, 2006). Deviance reduction and odds ratios were computed for each independent variable as it was added to the reduced multiple-variable model. Similarly, the parameter estimates and their standard error were estimated for independent variables in the models, and the odds ratio was obtained by exponentiating the parameter estimates for comparing the effect based on a reference point. The deviance, the logarithm of the ratio of two likelihoods, was used to compare the single- and multiple-variable models. The significance of the variable was assessed by comparing the likelihood ratio tests' difference with the Chi-square (χ^2) value (McCullagh & Nelder, 1989).

RESULTS AND DISCUSSION

Characteristic features of surveyed fields

A woolly apple aphids, codling moths, and mealybugs survey was conducted in 164 fields of five potential apple-growing FAs that found an altitudinal range between 2234 and 3058 m a.s.l., in which 30.49 and 69.51% of fields were situated at an altitude of ≤2500 and >2500 m a.s.l. in that order. Inspected districts are characterized by various field management practices (tree and nutrient management), land uses, soil and water shade management practices, and gentle slopes to rugged mountains. About 60.98% of fields in the study areas were inspected during off-season, while the remaining fields (39.02%) were covered during the main seasons. The FA's inspected apple field sizes varied from 100 to 15,000 m^2 for farmers' orchards to 200 to 30,000 m^2 for private farms' orchards (Kalehiwot Church), and the majority (75.61%) of the field sizes were over >250 m^2 across districts (Table 1). During the survey periods, it was observed that there were more than hundred apple varieties; however the dominant apple varieties grown by farmers were bonded red, Chencha gala, golden delicious, chrispine, fear, grani, Jona gorud, bartiletic fear, and red delicious, which were cultivated on farmer fields (97.56%) and private farms (2.44%) in the assessed total fields. Of these varieties, bonded red, crispine, and grani were the most important varieties preferred by farmers and consumers due to their attractive color, tasty, and its high productivity per tree. Farmers sourced apple seedlings mainly from nongovernmental organizations (93.90%); Bureau of Agriculture sources constituted only 6.10% of apple seedlings recorded (Table 1).

Table 1. Categorization of variables and independent variables by insect pest contingency table for logistic regression analysis of the distribution and incidence of apple wooly aphids, codling moths, and mealybug occurrence in the study areas of southern Ethiopia (n = 164) during the 2021 and 2022 cropping years.

Variables	Variable class	Number of fields	Aphid incidence (%)		Codling moth Incidence (%)		Mealybug incidence (%)	
			≤15	≥15	≤40	>40	≤20	>20
Years	2021	82	45	37	60	22	68	14
	2022	82	50	32	74	8	74	8
Seasons [a]	Main rainy season	64	40	20	36	28	30	34
	Off-season	100	45	55	48	52	50	50
Age of trees	≤5 years	2	2	0	2	0	1	1
	5 – 10 years	20	13	7	18	2	18	2
	10 – 15 years	48	23	25	39	9	43	5
	>15 years	94	59	35	76	18	80	14
Weed infestation [b]	Low levels	96	71	25	64	32	77	19
	Intermediate	40	30	10	28	12	37	3
	High levels	30	11	19	7	23	30	0
Survey sites	Farmer field	160	94	66	130	30	138	22
	Private farm	4	3	1	4	0	4	0
Field size	< 250 m^2	40	23	17	30	10	34	6
	≥ 250 m^2	124	80	44	99	25	111	13
Plant density [c]	≤ 8 plants in 100 m^{-2}	98	40	58	75	24	80	18
	> 8 plants in 100 m^{-2}	68	38	30	46	22	55	13
Plant material sources	Non-government	154	100	54	90	64	112	42
	Bureau of Agriculture	10	0	10	10	0	6	0
Growth stages	Flowering	10	6	4	7	3	6	4
	Fruit development	86	47	39	77	9	82	4
	Fruit maturity	68	45	23	52	16	51	17
Altitude (m a.s.l.) [d]	≤2500	50	34	130	42	8	46	4
	>2500	114	69	45	92	22	97	17
Cropping systems [e]	Sole cropped	46	29	17	28	18	34	12
	Intercrops with enset	18	15	3	16	2	13	5
	Intercrops with vegetables	38	23	16	34	4	36	2
	Intercrops with cereals	16	10	6	16	0	16	0
	Intercrops with legumes	12	4	8	9	3	12	0
	Intercrops with Irish potato	34	15	19	28	6	31	3
Tree management	Composting	26	11	15	23	3	8	3
	Pruning	26	17	9	21	5	22	4
	Composting and pruning	96	54	42	76	20	81	15
	Not practiced	16	7	9	12	4	16	0

[a]Main rainy season refers to crop production periods under heavy and frequent rainy times, and off season denotes dry or sunny periods (little or no rain at all) of the production year under Ethiopian conditions. [b]Weed infestation levels were recorded as low, intermediate, and high, indicating little weeds or weed-free, few weeds, and high weed infestation levels or no weeding, respectively. [c] Plant density was determined as the number of plants per 100 m^2 in a space size of 3 m × 4 m for a unit plant. [d]Attitudinally, areas with 2001–2500 and >2500 m a.s.l. are classified as highland (cool/semi-humid) and extreme highland (cool/humid) in that order in Ethiopia (Amede *et al.*, 2015). [e]Intercrops with vegetables, cereals, and legumes refer to fields with apple plus onion, scaly leaf cabbage, head cabbage, beat root, and rapeseed, apple plus barley, triticale, and wheat, and apple plus Faba bean and field pea, respectively.

Out of the assessed apple fields, 57.32% of the fields were planted before 15 years ago, while 29.27% between 10 and 15 years ago, 12.20% between 5 and 10 years ago, and only 1.21% were planted recently. Various growth stages, such as flowering, fruit development, and fruit maturity stages, were recorded during the survey periods, which corresponded with 6.10, 52.44, and 41.46% of the growth stages, respectively. Upon field observation, apple fields were found at various plant densities, such as 3 to 12 plants in 100 m^{-2}, of which about 59.77% and 40.23% fields constituted <8 and >8 plants in 100 m^{-2} (Table 1). During the survey, it was observed that inorganic fertilization of apple trees was not common, i.e., growers never used inorganic fertilizer; rather, the soil of their fields was mainly maintained with organic fertilizers, like farmyard manure, composting, and organic mulching, and fertilization was practiced twice per year. In this connection, field assessment indicated that apple trees were managed with management practices. About 58.54% of the apple growers' fields were managed with a combination of composting and pruning, while 15.85%, 15.85%, and 9.76% were shared with composting, pruning, and an unmanaged one, respectively (Table 1). In the same manner, different cropping systems were encountered during the survey: sole cropped and intercropped with various annual and perennial crops. Enset, vegetables (onion, scaly leaf cabbage, head cabbage, beat root, and rapeseed), cereals (barley, triticale, and wheat), legumes (Faba bean and field pea), Irish potato, and some beneficial agroforestry trees constituted intercropping components. Accordingly, about 28.05, 10.98, 23.07, 9.77, 7.32, and 20.81% of apple fields were inseminated by sole cropping and intercropped with enset, vegetables, cereals, legumes, and Irish potato in that order of presentation.

Regarding weeds, more than 20 various weed species, which differed in population densities, life cycle (annual, biennial, or perennial type), and life forms (grasses, sieges, herbs, and bush types), were recorded. Of which, low levels of weed infestations roofed about 58.54% of the total inspected apple fields, whereas the remaining 23.39 and 18.07% of the total apple fields were at intermediate and high levels of weed infestation, implying that weeding practices are more or less common activities in the study areas. Common weed flora that were observed during the study were *Cyperus esculantum*, *Cyperus rotundus*, *Guizotia scabra*, *Digitaria ternate*, *Drymaria cordata*, *Brachiaria eruciformis*, *Guizotia scabra*, *Galinsoga parviflora*, *Bidens pilosa*, *Amaranthus graecizans*, *Trifolium rueppellianum*, *Xanthium strumarium*, *Setaria pumila*, *Eragrostis cilianensis*, *Echinochloa colonum*, *Digitaria horizontalis*, and *Rumex abyssinica*. Field observation also indicated that the occurrence of woolly apple aphids, codling moths, and mealybugs was relatively higher in 2021 than in 2022. Moreover, the population dynamics of these insect pests significantly fluctuated over years, seasons within a year, and biophysical factors. Apple producers discovered that they needed to use cultural practices that relied entirely on the removal of infective leaves, dead branches, and sanitation to manage the insects. No insecticidal management was observed during the surveying periods. The other restraints and still devastating biotic restraints, such as apple scab, powdery mildew, anthracnose, root rot caused by complexes of pathogens, and viral diseases, were found year after year, and these factors, along with abiotic factors like climate change and soil acidity problems, significantly influenced the productivity of the crop in the study areas.

Biophysical and temporal factors influenced insect pest distributions and incidences

Field observation indicated that woolly apple aphids and mealybugs attack trunks, branches, stems, twigs, leaf petioles, and fruit stalks, and as a result, the fruits are undersized and malformed on heavily infested trees and have poor quality and not good taste. During the survey, it was observed that codling moths were not observed in the main rainy season, suggesting the insect pest presence might be associated with the growth stages of fruit development and maturity time. In the off-season, the larvae of codling moth tunnel through the fruits via eating away the pulp, filling the tunnels with frass (excrement), and hence, this makes the fruits unsuitable for human consumption, reducing marketability and farmers' income. Results showed that woolly apple aphids, codling moths, and mealybugs were widely distributed with various degrees of prevalence and incidences in the study areas over the years as well as seasons within the year, with higher in 2021 than 2022, irrespective of biophysical and temporal changes. The mean prevalence of woolly apple aphids, codling moths, and mealybugs was higher in 2021 (90.18, 75.61, and 50.45%) than in 2022 (70.26, 54.15, and 36.48%) in that order. Similarly, incidences of woolly apple aphids, codling moths, and mealybugs were recorded at about 57.56, 54.93, and 33.29% in 2021, and 37.01, 40.78%, and 21.23% in 2022, respectively, in the study areas. The results of incidences against other biophysical and temporal factors for woolly apple aphids, codling moths, and mealybugs are presented in Table 2.

A maximum mean incidence of woolly apple aphids (37.57 ± 0.0 and 12.64 ± 0.0%) and codling moths (38.61 ± 2.86 and 22.83 ± 2.93%) were recorded during off season, while the lowest mean woolly apple aphid incidence (17.01 ± 0.0 and 8.01 ± 0.0%) was obtained from the main rainy season in 2021 and 2022 cropping years, respectively. However, there was no recording of codling moths in the main rainy season in cropping years (Table 2). Mealybug incidence was in contrast to the phenomena observed in woolly aphids and codling moths for the seasons within the years during the study. These were explained by the higher mealybug incidence of 33.61±1.89 and 15.20 ± 1.45% noticed from the main season than that of off season (21.53±1.16% in 2021 and 10.24 ± 1.14% in 2022) (Table 2). In the same manner, cultivation of apples at an altitude of ≤2500 m a.s.l. exhibited the maximum mean incidences of woolly apple aphids (16.80 ± 3.95 and 13.86 ± 2.59%) and codling moths (28.42 ± 3.81 and 16.40 ± 4.08%) compared with cultivation at higher altitudes (>2500 m a.s.l.), in which about 14.32 ± 3.03 and 12.80 ± 3.39%, and 21.20 ± 5.67 and 13.68 ± 2.42% incidences were recorded for woolly aphids and codling moths in 2021 and 2022, respectively. The reverse was true for mealybug, in which the higher mean incidence (15.79 ± 3.27% in 2021 and 13.86 ± 2.59% in 2022) was recorded from an altitude of >2500 m a.s.l. than the ≤2500 m a.s.l., 5.20 ± 2.72% in 2021 and 3.20 ± 2.72% in 2022 (Table 2).

Table 2. Mean incidence (mean ± SE) of wooly apple aphid, codling moth, and mealybug for different biophysical and temporal factors in the study areas of southern Ethiopia during the 2021 and 2022 main rainy and off seasons.

Variables	Variable classes	Woolly apple aphid incidence (%)		Codling moth incidence (%)		Mealybug incidence (%)	
		2021	2022	2021	2022	2021	2022
Seasons [a]	Main rainy season	17.01 ± 0.0	8.01 ± 0.0	0.00 ± 0.00	0.00 ± 0.00	33.61±1.89	15.20 ± 1.45
	Off-season	37.57 ± 0.0	12.64 ± 0.0	38.61 ± 2.86	22.83 ± 2.93	21.53±1.16	10.24 ± 1.14
Age of trees	≤5 years	0.00 ± 0.0	0.0 ± 0.0	9.00 ± 0.00	0.00 ± 0.00	4.00 ± 3.05	0.00 ± 0.0
	5 – 10 years	23.00 ± 9.67	14.00 ± 7.48	14.00 ± 5.42	12.98 ± 2.68	11.25 ± 4.01	3.00 ± 3.0
	10 – 15 years	17.50 ± 4.18	16.25 ± 3.94	25.42 ± 6.02	13.00 ± 5.78	14.26 ± 3.63	7.50 ± 3.09
	>15 years	14.89 ± 3.02	12.34 ± 2.57	27.87 ± 4.20	13.40 ± 2.71	50.0.0 ± 00	7.66 ± 2.60
Weed infestation [b]	Low levels	13.50 ± 3.35	12.66 ± 5.73	15.74 ± 4.37	14.50 ± 4.07	4.67 ± 1.92	2.50 ± 1.60
	Intermediate	17.33 ± 5.81	13.00 ± 3.49	22.00 ± 6.19	18.00 ± 5.54	7.50 ± 3.39	4.00 ± 1.90
	High levels	17.45 ± 3.54	14.04 ± 2.78	30.50 ± 6.56	20.75 ± 4.14	8.23 ± 3.90	9.78 ± 2.91
Survey sites	Farmer field	16.63 ± 2.46	13.88 ± 2.10	26.87 ± 3.21	14.88 ± 2.12	12.88 ± 2.52	7.13 ± 1.82
	Private farm	10.00 ± 10.0	0.0 ± 0.0	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.0	0.00 ± 0.0
Field size	< 250 m^2	12.20 ± 1.23	7.10 ± 1.10	14.70 ± 1.40	6.20 ± 1.44	21.70 ± 0.98	6.14 ± 1.34
	≥ 250 m^2	14.88 ± 1.32	13.08 ± 1.03	25.90 ± 1.92	16.77 ± 1.20	27.35 ± 1.60	10.23 ± 1.07
Plant density [c]	≤ 8 plants in 100 m^{-2}	9.70 ± 1.44	10.30 ± 0.90	12.10 ± 3.00	8.40 ± 2.20	15.94 ± 1.55	9.06 ± 1.39
	> 8 plants in 100 m^{-2}	18.06 ± 0.96	15.49 ± 3.35	18.12 ± 1.30	13.50 ± 1.10	25.43 ± 3.06	15.60 ± 1.07
Plant material sources	Non-government	16.98 ± 1.07	8.90 ± 1.25	22.22 ± 3.66	14.34 ± 1.14	28.54 ± 1.31	17.56 ± 1.76
	Bureau of Agriculture	11.00 ± 1.01	4.51 ± 2.04	13.55 ± 1.12	10.23 ± 2.13	23.06 ± 1.25	10.52 ± 1.48
Growth stages	Flowering	26.00 ± 16.6	20.00 ± 12.25	0.00 ± 0.00	0.00 ± 0.00	6.51 ± 1.99	3.95 ± 1.21
	Fruit development	18.84 ± 3.13	13.72 ± 2.86	42.00 ± 12.8	24.00 ± 10.29	14.00 ± 8.72	9.71 ± 3.76
	Fruit maturity	12.06 ± 3.55	12.35 ± 3.02	30.59 ± 5.69	17.35 ± 3.46	20.00 ± 5.03	14.00 ± 8.72
Altitude (m a.s.l.) [d]	≤2500	16.80 ± 3.95	13.86 ± 2.59	28.42 ± 3.81	16.40 ± 4.08	5.20 ± 2.72	3.20 ± 2.72
	>2500	16.32 ± 3.03	12.80 ± 3.39	21.20 ± 5.67	13.68 ± 2.42	15.79 ± 3.27	13.86 ± 2.59
Cropping systems [e]	Sole cropped	24.12 ± 5.88	20.59 ± 5.03	35.00 ± 14.8	16.84 ± 4.05	24.35 ± 5.82	13.48 ± 4.85
	Intercrops with enset	6.67 ± 4.71	5.56 ± 3.77	20.00 ± 9.57	15.56 ± 5.56	18.89 ± 10.06	6.67 ± 4.71
	Intercrops with vegetables	15.26 ± 4.67	12.11 ± 4.81	14.21 ± 4.21	13.48 ± 4.34	4.74 ± 3.45	4.74 ± 3.45
	Intercrops with cereals	17.50 ± 7.26	16.67 ± 6.15	8.75 ± 4.41	0.00 ± 0.00	3.75 ± 2.63	3.75 ± 2.63
	Intercrops with legumes	16.67 ± 6.15	13.04 ± 3.74	43.04 ± 6.27	21.67 ± 7.49	0.00 ± 0.0	0.00 ± 0.0
	Intercrops with Irish potato	15.22 ± 5.29	10.00 ± 6.82	25.29 ± 7.28	13.53 ± 4.77	10.59 ± 4.41	4.71 ± 2.29
Tree management	Composting	16.92 ± 4.58	12.31 ± 4.41	26.15 ± 8.28	15.00 ± 2.78	14.37 ± 3.48	6.92 ± 4.72
	Pruning	17.69 ± 8.26	8.75 ± 4.79	26.47 ± 4.41	13.85 ± 4.88	6.15 ± 4.01	6.67 ± 2.37
	Composting and pruning	16.25 ± 3.20	7.79 ± 2.73	23.08 ± 7.01	10.00 ± 4.80	3.75 ± 2.63	3.75 ± 2.63
	Not practiced	18.00 ± 5.34	13.08 ± 6.64	30.00 ± 8.45	20.00 ± 8.01	17.69 ± 7.43	10.00 ± 5.19

[a]Main rainy season refers to crop production periods under heavy and frequent rainy times, and off season denotes dry or sunny periods (little or no rain at all) of the production year under Ethiopian conditions. [b]Weed infestation levels were recorded as low, intermediate, and high, indicating little weeds or weed-free, few weeds, and high weed infestation levels or no weeding, respectively. [c] Plant density was determined as the number of plants per 100 m^2 in a space size of 3 m × 4 m for a unit plant. [d]Attitudinally, areas with 2001–2500 and >2500 m a.s.l. are classified as highland (cool/semi-humid) and extreme highland (cool/humid) in that order in Ethiopia (Amede *et al.*, 2015). [e]Intercrops with vegetables, cereals, and legumes refer to fields with apple plus onion, scaly leaf cabbage, head cabbage, beat root, and rapeseed, apple plus barley, triticale, and wheat, and apple plus Faba bean and field pea, respectively.

During the surveyed cropping years as well as seasons within the year in various altitudinal ranges, woolly apple aphids, codling moths, and mealybugs were widely distributed in all surveyed areas, although variability between the years and seasons within the year was observed due to the influence of biophysical factors. The spatiotemporal differences in the prevalence and incidences of the aforementioned insects in 2021 and 2022 might be attributed to variability in weather conditions (Figure 1) and altitudinal ranges of assessed apple fields, along with other factors (Tables 1 and 2). In the current study, it was observed that the highest incidences of apple aphids and codling moths were recorded off seasons than main rainy seasons and low than higher altitudes, implying the incident of two insect pests might favor dry climate and cool conditions over relatively wet and high rainy conditions and discourage their incidents at higher altitudes. In contrast to these insects, mealybug incidence was higher during main rainy seasons than off seasons and at high altitude, suggesting the occurrence of mealybugs significantly influenced by these factors and favored by wet conditions and altitudinal increments. The present study agreed with other reports presented in many parts of the world, which indicated that weather variables and altitudinal ranges significantly influenced the dynamics of woolly apple aphids (Gresham, 2013; Stokwe & Malan, 2016), codling moths (Zhao *et al.*, 2015; Etienne *et al.*, 2024), and mealybugs (Babu & Azam, 1987; García-Álvarez *et al.*, 2014) across surveyed apple fields over the years and cultivating seasons where the insect pests were found severely in the aforementioned weather and altitudinal factors in the present study and caused considerable destruction for the apple orchards and yield losses. A report by Mengesha *et al.* (2021), Zhang *et al.* (2018) and Courson *et al.* (2022) also indicated that weather variables and topographic features of a given region, along with seasonal variation within the year, were the main drivers of insect pest occurrence in arable agriculture fields.

In 2021, apple fields was inspected in farmer fields (16.63 ± 2.46 and 26.87 ± 3.21%), > 250 m^2 field size (14.88 ± 1.32 and 25.90 ± 1.92%), > 8 plants in 100 m^2 plant density (18.06 ± 0.96 and 18.12 ± 1.30%), age of trees [5–10 years (23.00 ± 9.67%), >15 years (27.87 ± 4.20%)], growth stage [flowering (26.00 ± 16.6%), fruit development (42.00 ± 12.80%)], and plant material sourced from non-government organization (16.98 ± 1.07 and 22.22 ± 3.66%) recorded the highest mean woolly apple aphid and codling moth incidences in that order compared with the remaining counterpart variable classes. Of the assessed apple fields, farmer fields (12.88 ± 2.52%) having a field size of > 250 m^2 (21.70 ± 0.98%), > 8 plants in 100 m^2 plant density (25.43 ± 3.06%), at fruit maturity growth stage (20.00 ± 5.03%), and plant material sourced from non-government organizations (28.54 ± 1.31%), which was planted >15 years (50.00 ± 0.0%) received the highest mealybug incidence as compared with their respective variable classes in 2021 (Table 2). In the same year, apple farms found with intercropped [enset (6.67 ± 4.71%), cereals (8.75 ± 4.41%) and legumes (0.00 ± 0.0%)], tree management with composting and pruning (16.25 ± 3.20, 7.79 ± 2.73, and 3.75 ± 2.63%), and low weed infestation (13.50 ± 3.35, 15.74 ± 4.37, and 4.67 ± 1.92%) contributed to low levels of mean woolly apple aphid, codling moth, and mealybug incidences, respectively, as compared with their respective variable classes (Table 2). Implying that factors like intercropping with enset (for woolly apple aphids and codling moths) or legumes (for mealybugs), proper weeding (low infestation), and tree management via composting and pruning reduced mean woolly apple aphid, codling moth, and mealybug incidences by 72.35, 79.67, and 100%, 22.64, 48.39, and 74.44%, 23.07, and 62.50%, respectively, compared with variable class that showed highest incidences for the respective insects in 2021. Similar trends were traced for the2022 cropping year for the studied biophysical and temporal factors.

The seasonal variation and altitude alone influenced the occurrence and dispersal of woolly apple aphids, codling moths, and mealybugs, as the results showed, but when combined with other biophysical factors, particularly high plant density, sole cropping, inappropriate choice of intercrop crops, high weed population, improper tree management, and many other factors, it resulted in a highly significant effect on the aforementioned insect distributions and associated yield losses. In this study, the incidences of these insects were relatively higher fields inspected with high plant density, sole cropping and intercrops with hosts of each insect, high weed population, and improper tree management across the study areas over years as well as seasons within the year (Tables 2-4).

Table 3. Mean number of individual insects per apple tree (mean + SE) for woolly apple aphid, codling moth, and mealybug in various independent variables in the study areas of southern Ethiopia in the main rainy and off seasons of 2021 and 2022.

Variables	Variable classes	Woolly apple aphids		Codling moths		Mealybugs	
		2021	2022	2021	2022	2021	2022
Seasons [a]	Main rainy season	12.03 ± 4.21	7.09 ± 3.67	0.00 ± 0.00	0.00 ± 0.00	17.20 ± 0.98	20.45 ± 0.01
	Off-season	16.03 ± 5.32	12.35 ± 2.81	5.06 ± 0.92	3.90 ± 0.46	14.10 ± 1.09	10.41 ± 0.20
Age of trees	≤5 years	0.0 ± 0.0	0.0 ± 0.0	1.70 ± 0.00	0.00 ± 0.00	4.66 ± 0.66	0.00 ± 0.00
	5 – 10 years	9.70 ± 2.68	4.10 ± 1.42	20.81 ± 4.07	9.55 ± 2.37	5.54 ± 0.74	1.10 ± 0.43
	10 – 15 years	7.71 ± 1.82	1.87 ± 1.00	26.11 ± 6.03	10.30 ± 5.32	8.00 ± 0.00	2.00 ± 0.34
	>15 years	7.72 ± 1.12	3.02 ± 0.82	32.30 ± 9.41	14.25 ± 3.64	8.10 ± 3.31	3.85 ± 0.39
Weed infestation [b]	Low levels	6.87 ± 2.06	0.60 ± 0.42	10.53 ± 3.84	8.62 ± 1.92	4.10 ± 1.34	1.60 ± 0.34
	Intermediate	7.29 ± 1.16	2.27 ± 1.11	21.35 ± 6.60	12.90 ± 4.19	5.47 ± 0.66	1.75 ± 0.26
	High levels	9.95 ± 1.89	3.87 ± 0.90	22.87 ± 8.55	15.87 ± 5.91	6.80 ± 0.87	2.05 ± 0.82
Survey sites	Farmer field	7.90 ± 0.92	3.00 ± 3.00	22.81 ± 3.16	11.26 ± 1.87	5.40 ± 0.54	1.78 ± 0.25
	Private farm	6.50 ± 2.50	0.0 ± 0.0	0.00 ± 0.00	0.00 ± 0.00	0.0 ± 0.0	0.00 ± 0.0
Field size	< 250 m^2	6.58 ± 2.59	1.77 ± 0.90	20.02 ± 2.96	4.34 ± 1.02	15.15 ± 2.06	4.10 ± 1.26
	$\geq$ 250 m^2	10.90 ± 1.90	2.20 ± 1.07	30.20 ± 2.40	10.46 ± 0.11	20.27 ± 1.42	10.20 ± 1.30
Plant density [c]	$\leq$ 8 plants in 100 m^{-2}	10.03 ± 1.32	1.80 ± 1.02	7.34 ± 2.58	5.19 ± 1.19	5.46 ± 2.20	4.26 ± 1.40
	> 8 plants in 100 m^{-2}	15.33 ± 1.25	4.44 ± 1.99	11.22 ± 1.08	10.38 ± 1.01	7.20 ± 1.55	2.32 ± 2.76
Plant material sources	Non-government	10.48 ± 1.11	3.90 ± 1.05	32.03 ± 1.56	10.05 ± 1.20	12.06 ± 1.54	6.70 ± 1.09
	Bureau of Agriculture	5.50 ± 1.44	1.99 ± 1.15	23.50 ± 4.45	4.93 ± 2.03	5.50 ± 3.74	1.58 ± 4.00
Growth stages	Flowering	8.80 ± 4.59	3.35 ± 0.89	0.00 ± 0.00	0.00 ± 0.00	5.00 ± 1.26	1.42 ± 0.26
	Fruit development	8.03 ± 1.43	2.29 ± 0.81	18.29 ± 4.49	11.53 ± 2.93	5.08 ± 0.87	2.20 ± 0.80
	Fruit maturity	7.63 ± 1.19	1.20 ± 1.20	28.74 ± 4.51	10.39 ± 2.62	5.65 ± 0.73	2.21 ± 0.49
Altitude (m a.s.l.) [d]	≤2500	9.20 ± 1.68	4.28 ± 1.35	31.32 ± 5.96	13.24 ± 364	3.52 ± 0.75	1.61 ± 0.26
	>2500	7.28 ± 1.05	2.12 ± 0.58	20.21 ± 3.63	10.00 ± 2.11	6.19 ± 0.66	2.20 ± 0.59
Cropping systems [e]	Sole cropped	11.56 ± 3.45	6.40 ± 0.99	31.66 ± 13.2	19.67 ± 6.14	7.47 ± 1.29	3.25 ± 0.84
	Intercrops with enset	4.63 ± 1.18	1.89 ± 1.27	7.67 ± 6.56	6.74 ± 3.03	4.96 ± 0.73	1.89 ± 0.59
	Intercrops with vegetables	6.44 ± 1.64	2.95 ± 1.32	22.63 ± 7.08	9.79 ± 4.73	5.42 ± 1.39	2.09 ± 0.51
	Intercrops with cereals	8.95 ± 1.98	4.25 ± 2.52	23.75 ± 7.78	0.00 ± 0.00	6.50 ± 1.12	0.67 ± 0.33
	Intercrops with legumes	10.83 ± 3.03	6.33 ± 2.98	31.35 ± 8.27	9.65 ± 3.93	0.00 ± 0.0	0.00 ± 0.0
	Intercrops with Irish potato	7.12 ± 1.97	2.12 ± 1.01	11.00 ± 4.08	7.56 ± 4.35	2.22 ± 1.12	1.88 ± 0.59
Tree management	Composting	7.31 ± 1.87	2.13 ± 1.63	25.68 ± 4.09	16.77 ± 5.65	6.00 ± 1.06	2.46 ± 1.06
	Pruning	7.08 ± 1.89	2.08 ± 1.11	25.00 ± 12.3	9.25 ± 1.96	5.60 ± 0.78	1.85 ± 0.75
	Composting and pruning	5.63 ± 3.01	1.92 ± 0.51	11.38 ± 7.22	5.69 ± 3.65	3.15 ± 0.88	1.56 ± 0.25
	Not practiced	8.60 ± 1.27	7.08 ± 2.56	27.23 ± 7.54	21.07 ± 10.33	10.63 ± 1.25	4.00 ± 0.50

[a] Main rainy season refers to crop production periods under heavy and frequent rainy times, and off season denotes dry or sunny periods (little or no rain at all) of the production year under Ethiopian conditions. [b] Weed infestation levels were recorded as low, intermediate, and high, indicating little weeds or weed-free, few weeds, and high weed infestation levels or no weeding, respectively. [c] Plant density was determined as the number of plants per 100 m^2 in a space size of 3 m × 4 m for a unit plant. [d] Attitudinally, areas with 2001–2500 and >2500 m a.s.l. are classified as highland (cool/semi-humid) and extreme highland (cool/humid) in that order in Ethiopia (Amede et al., 2015). [e] Intercrops with vegetables, cereals, and legumes refer to fields with apple plus onion, scaly leaf cabbage, head cabbage, beat root, and rapeseed, apple plus barley, triticale, and wheat, and apple plus Faba bean and field pea, respectively.

The high plant density favored the studied insects through regulating the microclimate around the tree and facilitating the invasion by other plant pathogens, while sole cropping and intercropping with host plants increased the chances of egg deposition and recurrent occurrences of the insects through the growing seasons as well as year after year in the study areas. Similarly, the presence of a high weed population does have an unavoidable effect on insect infestations and disease development. Moreover, weeds compete with the crop for resources available, harbor other insect pests along with vector-borne diseases, and have the fastest rate of reproduction. This might be partly due to reduced crop vigor and associated yield losses as a result of intensive competition for available resources, which in turn could predispose the plant to diseases. In the study areas, it was observed that apple tree management was not common, and in some fields, highly populated plants caused restrictions on movement within the fields. Accordingly, tree management was one of the most significant biophysical factors that had a high association with the studied insect pest spates in both cropping years as well as seasons within the year. Proper tree management could reduce competition for growth resources (light, water, and nutrients) and lead to more vigorous growth, which helps the plant resist insect pests, pathogenic effects, and harsh environmental conditions. A study by Stokwe & Malan (2016) and Happe *et al.* (2018) for woolly apple aphids, Adom *et al.* (2021) and Etienne *et al.* (2024) for codling moths, and de Azevedo *et al.* (2015) and Tebkew & Chris (2017) for mealybugs indicated that good cultural practices such as proper plant density, intercropped with non-host crops, good weed management, and tree management via pruning and composting reduces available resource competition and increases fruit size, and suppresses insect establishment due to a reduction in cross contamination through increased spatial distance between the standing plants, the chance of insect pest outbreaks, and efficient use of growth resources available.

Number of individual insects as influenced by biophysical and temporal factors

During the study periods, it was observed that there were different levels of NIPP for woolly apple aphids, codling moths, and mealybugs noted among the study areas (Table 3). Results indicated that higher mean woolly apple aphids, codling moths, and mealybugs NIPP were obtained in 2021 than in 2022 in this study. Accordingly, mean NIPP of woolly apple aphids, codling moths, and mealybugs were 22.15, 14.80, and 12.81 in 2021 and 15.10, 9.16, and 7.70 in 2022, respectively, among study sites. Table 3 displays the NIPP results for the insects under study in comparison to other biophysical and temporal factors. Similarly, higher mean NIPP was obtained during off season for woolly apple aphids (16.03 ± 5.32 and 12.35 ± 2.81) and codling moths (5.06 ± 0.92 and 3.90 ± 0.46) than main rainy season for the two insects, in which higher mean NIPP for woolly apple aphids (12.03 ± 4.21 and 7.09 ± 3.67) and codling moths (0.0 ± 0.0 and 0.0 ± 0.0) was computed in 2021 and 2022, respectively. In contrast to woolly apple aphids and codling moths, mean NIPP values of 17.20 ± 0.98 (in 2021) and 20.45 ± 0.01 (in 2022) were recorded from the main rainy season rather than the off season (14.10 ± 1.09 in 2021 and 10.41 ± 0.20 in 2022) (Table 3).

Apple farms inspected at ≤2500 m a.s.l. (9.20 ± 1.68, 31.32 ± 5.96 and 3.52 ± 0.75) that found in tree age of 5 – 10 years (9.70 ± 2.68) and >15 years (32.30 ± 9.41 and 8.10 ± 3.31), farmer fields (7.90 ± 0.92, 22.81 ± 3.16 and 5.40 ± 0.54), field size of > 250 m^2 (10.90 ± 1.90, 30.20 ± 2.40 and 20.27 ± 1.42), plant density of >8 plants in 100 m^2 (15.33 ± 1.25, 11.22 ± 1.08 and 7.20 ± 1.55), plant material sources from non-government organization (10.48 ± 1.11, 32.03 ± 1.56 and 12.06 ± 1.54), at growth stage of flowering (8.80 ± 4.59) and fruit maturity (28.74 ± 4.51 and 5.65 ± 0.73), sole cropped (11.56 ± 3.45, 31.66 ± 13.2 and 7.47 ± 1.29), and absence of tree management (8.60 ± 1.27, 27.23 ± 7.54 and 10.63 ± 1.25) exhibited the highest mean NIPP of woolly apple aphids, codling moth, and mealybugs in that order as compared with their respective variable classes in 2021. In the study areas, closely similar trends were noted with respect to NIPP of woolly apple aphids, codling moths, and mealybugs against studied biophysical and temporal factors in 2022 (Table 3).

The current survey found that woolly apple aphid, codling moth, and mealybug NIPP varied in the study areas in the two years as well as across seasons within the year. In 2021, the NIPP of the studied insect pests was considerably higher than in 2022. This might be due to the prevailing weather conditions along with altitudinal ranges, plant density, cropping systems, weed infestation, tree management, and other agronomic practices significantly influencing the population dynamics of the studied insect pests (Tables 1 and 3). In 2021, there was relatively less precipitation, high mean temperatures, and low relative humidity than in 2022 in the study areas. As a result, the weather conditions were more favorable for woolly apple aphids, codling moths, and mealybug fast reproduction, development, field infestation, and their population number per tree in 2021. This suggests that the relatively dry weather is more favorable for these insect pests. Comparatively, significantly lower NIPPs were observed in 2022; the reasons might be lesser precipitation, warm temperatures, and low humidity, along with good field management interventions. Dry conditions and proper agronomic practices might hamper the outbreaks and development of insect pests. Previous scholars also reported that such circumstances were major responsible factors for the high population dynamics of these insect pests. Walker *et al.* (1988) and Vashisth *et al.* (2024) and for woolly apple aphids, Hagley (1972) and Adom *et al.* (2021) for codling moths and García-Álvarez *et al.*, 2014) and Sá and Oliveira (2021) for mealybugs reported that high humidity (>60% during infection), high rainfall (> 1000 mm annually), and temperature (13–22 °C) at low to high altitudes, along with cultivar susceptibility, inappropriate crop field management, and absence of pest management, had contributed to outbreak, fast reproduction, development, widespread infestation, and their population dynamics. This phenomenon, such as favorable weather conditions, cultivar susceptibility, poor cropping systems, and inappropriate crop field and pest management, was true in the study areas, especially during the 2021 crop year.

Table 4. Logistic regression analyses for incidences of aphids, codling moths, and mealybugs of apple fruit and likelihood ratio tests on independent variables in the study areas of southern Ethiopia in the 2021–2022 main rainy and off seasons.

Independent variable	df	Woolly apple aphids incidence, LRT				Codling moths incidence, LRT				Mealybugs incidence, LRT			
		Type 1 analysis, VEF		Type 3 analysis, VEL		Type 1 analysis, VEF		Type 3 analysis, VEL		Type 1 analysis, VEF		Type 3 analysis, VEL	
		DR	Pr > χ^2	DR	Pr > χ^2	DR	Pr > χ^2	DR	Pr > χ^2	DR	Pr > χ^2	DR	Pr > χ^2
Years	1	27.58	<0.0001	24.50	<0.0001	350.49	<.0001	371.27	<0.0001	148.43	<0.0001	156.75	0.0001
Seasons	1	70.22	<0.0001	13.05	0.0019	14.68	0.0008	28.99	<0.0001	25.09	0.0044	10.16	<0.0001
Altitude	1	20.23	0.0041	12.53	0.0020	11.23	0.0008	21.37	0.0001	190.11	<0.0001	36.17	<0.0001
Survey sites	1	14.60	0.0001	65.90	<0.0001	176.50	<0.0001	137.80	0.0001	44.70	<0.0001	36.10	<0.0001
Field size	1	1.05	0.9890	2.26	0.5568	15.25	0.0001	0.50	0.0800	16.30	0.0063	3.00	0.0625
Plant density	1	0.09	0.0837	0.38	0.5651	3.44	0.0630	3.32	0.0727	2.58	0.0663	13.84	<0.0001
Plant material sources	1	9.43	0.0045	0.88	0.0601	10.10	0.0021	0.16	0.0962	3.14	0.1003	10.68	0.0062
Age of trees	3	126.13	<0.0001	82.13	<0.0001	164.60	<0.0001	17.37	0.0006	201.25	<0.0001	13.74	0.0033
Growth stages	2	77.67	<0.0001	115.98	<0.0001	212.67	<0.0001	185.00	<0.0001	479.41	<0.0001	107.73	<0.0001
Cropping systems	5	310.95	<0.0001	347.86	<0.0001	512.98	<0.0001	605.48	<0.0001	530.08	<0.0001	429.04	<0.0001
Weed infestation	2	76.95	<0.0001	92.40	<0.0001	27.71	<0.0001	44.27	<0.0001	251.36	<0.0001	144.53	<0.0001
Tree management	3	38.73	<0.0001	18.36	<0.0001	145.23	<0.0001	50.29	<0.0001	27.45	<0.0001	8.33	<0.0001

[a]LRT = likelihood ratio test; VEF = variable entered first into the model; VEL = variable entered last into the model; DR = deviance reduction; Pr = probability of an χ^2 value exceeding the deviance reduction; χ^2 = Chi-square; and df = degrees of freedom.

The study also recognized the importance of maintaining plant density, intercrops with non-host crops, low levels of weed infestation, and good tree management via composting and pruning as part of the crop management option to reduce woolly apple aphid, codling moth, and mealybug NIPP and field infestation. As a general principle, optimal plant density of any crop, crop diversification with non-hosts, fertilization, pruning, and weed management reduces plant stress, improves physiological resistance, and decreases insect pest risks. Conversely, cultivations of apples in the presence of high plant density and weed populations, sole cropping or intercropping with host crops, and poor tree and soil nutrient management are known to severely affect the crop and reduce the associated yield of the crop and favor the insect pest and fastest rate of reproduction (Happe *et al*., 2018; Adom *et al*., 2021; Etienne *et al*., 2024). Moreover, Tebkew & Chris (2017) reported that cropping history, cropping systems like crop diversification and rotation, and fluctuation of weather conditions influence population dynamics of insect pests and encourage the buildup of their predators. Population dynamics of woolly apple aphids (Tesfaye *et al*., 2012), codling moths (Brown & Tworkoski, 2004), and mealybugs (Tebkew & Chris, 2017) fluctuate significantly as the cropping season, field management practices, and weather variables change.

Association of independent variables with studied insect pests incidence

Since changes in any of the variables affected population dynamics in the insect pest incidence during the survey periods, association studies between the incidences of woolly apple aphids, codling moths, and mealybugs and independent variables were crucial. The association of all independent variables with mean incidences of woolly apple aphids, codling moths, and mealybugs in apple production is presented in Table 4. According to logistic regression analyses, years, seasons, altitude, survey sites, age of trees, growth stages, cropping systems, weed infestation, and tree management practices were the most important independent variables and exhibited a highly significant (P < 0.01 to 0.0001) association with mean woolly apple aphids, codling moth, and mealybug incidences when entered first (as a single variable) and last (as a multiple variable) into the model in that order (Table 4). However, field size, planting density, and plant material sources showed a non-significant (P > 0.05) association with the mean woolly apple aphid incidence in the model when entered both first and last into the model. Otherwise, when field size was entered as a single variable in the model, it exhibited a significant (P < 0.001) association with the incidences of codling moth and mealybug, but when entered last into the model, it lost its significance (P > 0.05) relationship with their incidences. Plant density and plant material sources lost their significant (P > 0.05) association with codling moth incidence when entered both first and last into the model. The same independent variables lost their significance (P > 0.05) association with mealybug incidence when entered first into the model, while they gained their importance (P < 0.001) with mealybug incidence when entered last into the model (Table 4). Even if survey site was significantly associated with the incidences of woolly apple aphids, codling moths, and mealybugs when entered first and last into the model, the variable lost its significance for association with the incidence in the reduced multiple variable model (Table 4).

Those independent variables that exhibited significant associations in single (first entered) and multiple (last entered) variable models for each of woolly apple aphids, codling moths, and mealybugs were further tested in the reduced multiple regression model to find out the contribution and magnitude of the risk factor of each variable class to aphids, codling moths, and

Table 5. Analysis of deviance, natural logarithms of odds ratio, and standard error of added independent variables in the reduced model of woolly apple aphid incidence (%) in the study areas of southern Ethiopia during the 2021 and 2022 main rainy and off seasons.

Independent variable [a]	Residual deviance [b]	df	LRT		Variable class	Estimate Log_e (Odds ratio) [d]	SE	Odds ratio
			DR	Pr > χ^2				
Intercept	3362.29	0	-	-		-3.2175	0.2958	0.0401
Years	2460.36	1	24.41	<0.0001	2021	0.8361	0.0448	2.3074
			-	-	2022	0*	-	1
Seasons	2021.01	1	50.13	<0.0001	Off-season	1.6044	0.1021	4.9749
			-	-	Main rainy season	0*	-	1
Altitude	1690.74	1	2.54	0.0347	>2500	-0.6524	0.0616	0.5208
			-	-	≤2500	0*	0.0000	1
Age of tree	1383.7	3	0.00	0.0084	5–10 years	1.2988	0.1098	3.6649
			10.36	<0.0001	10–15 years	0.4776	0.0751	1.6122
			15.76	<0.0001	>15 years	0.2247	0.0581	1.2519
			-	-	≤5 years	0*	-	1
Growth stages	1233.21	2	95.41	<0.0001	Fruit development	-0.726	0.1009	0.4838
			125.16	<0.0001	Fruit maturity	-0.9861	0.0945	0.3730
			-	-	Flowering	0*	-	1
Cropping systems	902.94	1	66.56	<0.0001	Intercrops with Irish potato	-0.5651	0.0693	0.5683
			258.32	<0.0001	Intercrops with enset	-1.8254	0.1136	0.1612
			79.55	<0.0001	Intercrops with vegetables	-0.6368	0.0714	0.5289
			26.70	<0.0001	Intercrops with cereals	-0.4644	0.0899	0.6285
			12.72	0.0004	Intercrops with legumes	-0.3429	0.0962	0.7097
			-	-	Sole cropped	0*	-	1
Weed infestation	552.47	2	6.10	0.0185	High levels	0.6543	0.1208	1.9238
			43.54	0.0456	Intermediate	0.3277	0.1213	1.3878
			-	-	Low levels	0*	-	1
Tree management	507.02	3	27.37	<0.0001	Not practiced	0.7179	0.1029	2.0501
			27.03	<0.0001	Pruning	0.6564	0.1394	1.9278
			28.01	<0.0001	Composting	0.6552	0.1324	1.9255
			-	-	Composting and pruning	0*	-	1

[a] Variables added into the model in order of presentation in Table. [b] Unexplained variations after fitting the model; [c] LRT = Likelihood ratio test; DR = deviance reduction; Pr = Probability of an χ^2 value exceeding the deviance reduction; χ^2 = Chi-square. [d] Estimates from the model with all independent variables added. * = Reference group. df = Degrees of freedom. SE = Standard error.

Table 6. Analysis of deviance, natural logarithms of odds ratio and standard error of codling moth incidence (%) and likelihood ratio test on independent variables in reduced regression model in the study areas of southern Ethiopia during 2021 and 2022 main rainy and off seasons.

Independent variable [a]	Residual deviance [b]	df	LRT		Variable class	Estimate Log_e (Odds ratio) [d]	SE	Odds ratio
			DR	Pr > χ^2				
Intercept	4095.04	0	-	-		-2.6508	0.1384	0.0706
Years	3411.15	1	357.67	<0.0001	2021	0.7903	0.0418	2.2041
			-	-	2022	0*	-	1
Seasons	2080.59	1	133.01	<0.0001	Main rainy season	-0.7312	0.0225	0.4813
			-	-	Off-season	0*	-	1
Altitude	1956.93	1	21.06	<0.0001	>2500	-0.8588	0.0588	0.4237
			-	-	≤2500	0*	0.0000	1
Age of tree	1456.03	3	12.83	0.0003	≤5 years	-0.5559	0.1552	0.5736
			0.13	0.0138	5–10 years	-0.0309	0.0841	0.9696
			2.97	0.0847	10–15 years	-0.0889	0.0516	0.9149
			-	-	>15 years	0*	-	1
Growth stages	1108.55	2	156.22	<0.0001	Fruit maturity	-1.1403	0.0912	0.3197
			57.36	<0.0001	Fruit development	-0.6206	0.0819	0.5376
			-	-	Flowering	0*	-	1
Cropping systems	684.88	1	47.98	<0.0001	Sole cropped	0.4562	0.0659	1.5781
			22.97	<0.0001	Intercrops with Irish potato	-0.3962	0.0827	0.6729
			10.02	0.0016	Intercrops with vegetables	-0.2321	0.0733	0.7929
			100.71	<0.0001	Intercrops with cereals	-1.3701	0.1365	0.2541
			229.25	<0.0001	Intercrops with legumes	1.2731	0.0841	3.5719
			-	-	Intercrops with enset	0*	-	1
Weed infestation	641.42	2	20.30	<0.0001	Low levels	-0.4701	0.1043	0.6249
			1.90	0.0480	Intermediate	-0.1419	0.1029	0.8677
			-	-	High levels	0*	-	1
Tree management	406.88	3	5.08	0.0242	Composting	-0.2745	0.1218	0.7599
			101.54	<0.0001	Pruning	-0.1836	0.1139	0.8323
			2.60	0.0169	Composting and pruning	-0.9406	0.0933	0.3904
			-	-	Not practiced	0*	-	1

[a] Variables added into the model in order of presentation in Table. [b] Unexplained variations after fitting the model; [c] LRT = Likelihood ratio test; DR = deviance reduction; Pr = Probability of an χ^2 value exceeding the deviance reduction; χ^2 = Chi-square. [d] Estimates from the model with all independent variables added. * = Reference group. df = Degrees of freedom. SE = Standard error.

Table 7. Analysis of deviance, natural logarithms of odds ratio and standard error of mealybug (%) of apple and likelihood ratio test on independent variables in reduced regression model in the study areas of southern Ethiopia during the 2021–2022 main rainy and off seasons.

Independent variable [a]	Residual deviance [b]	df	LRT DR	LRT Pr > χ^2	Variable class	Estimate Log_e (Odds ratio) [d]	SE	Odds ratio
Intercept	3835.40	0	-	-		-6.2446	0.2277	0.0019
Years	2898.38	1	150.94	<0.0001	2021	0.7113	0.0579	2.0366
			-	-	2022	0*	-	1
Seasons	2542.06	1	29.20	<0.0001	Main rainy season	1.2058	0.1151	3.3394
			-	-	Off-season	0*	-	1
Altitude	1775.28	1	34.54	<0.0001	≤2500	-0.4943	0.0841	0.6100
			-	-	>2500	0*	-	1
Age of tree	1249.19	3	0.63	0.0264	≤5 years	-0.142	0.1785	0.8676
			2.10	0.0477	5–10 years	-0.2094	0.1446	0.8111
			7.90	0.0049	10–15 years	0.22	0.0782	1.2461
			-	-	>15 years	0*	-	1
Growth stages	1084.87	2	29.79	<0.0001	Flowering	-0.7059	0.1293	0.4937
			0.15	0.6975	Fruit development	-0.1438	0.1125	0.8661
			-	-	Fruit maturity	0*	-	1
Cropping systems	843.09	1	57.45	<0.0001	Sole cropped	0.7036	0.0928	2.0210
			32.76	<0.0001	Intercrops with enset	0.5892	0.1029	1.8025
			60.87	<0.0001	Intercrops with vegetables	-1.2081	0.1548	0.2988
			1.40	0.2362	Intercrops with cereals	-0.1855	0.1566	0.8307
			0.00	0.9991	Intercrops with legumes	-4.5434	0.2196	0.0106
			-	-	Intercrops with Irish potato	0*	-	1
Weed infestation	685.09	2	74.38	<0.0001	High levels	1.2334	0.1430	3.4329
			3.92	0.0478	Intermediate	0.2927	0.1479	1.3400
			-	-	Low levels	0*	-	1
Tree management	599.87	3	2.03	0.0154	Not practiced	0.7114	0.1687	2.0368
			17.77	<0.0001	Composting	0.2734	0.1920	1.3144
			4.90	0.0269	Pruning	0.3989	0.1803	1.4902
			-	-	Composting and pruning	0*	-	1

[a]Variables added into the model in order of presentation in Table. [b]Unexplained variations after fitting the model; [c]LRT = Likelihood ratio test; DR = deviance reduction; Pr = Probability of an χ^2 value exceeding the deviance reduction; χ^2 = Chi-square. [d]Estimates from the model with all independent variables added. * = Reference group. df = Degrees of freedom. SE = Standard error.

mealybug pressure using the odds ratio. Accordingly, a reduced regression model analysis produced parameter estimates along with their standard errors and odds ratios for each of aphids (Table 5), codling moths (Table 6), and mealybugs (Table 7). In a reduced multiple-variable model, the deviation analysis of these independent variables discovered varying degrees of significance (*P* < 0.0001 to 0.01) of their associations with woolly apple aphids, codling moth, and mealybug incidences. In the model, the high probability of wooly aphids (>15%), codling moths (>40%), and mealybug (>20%) incidence was positively associated with years, seasons, altitude, age of tree, growth stages, cropping systems, wed infestation, and tree management practices (Tables 5-7).

The probability of the highest (>15%) wooly aphid incidence relation with 2021 year, off-season, 5-10 year age of tree, high weed infestation, and no tree management practiced was more than 2.31, 4.97, 3.66, 1.92, and 2.05 times risked than their references in the counterpart variable classes, while other independent variables were comparatively less risky related to the aforementioned variables for wooly aphid incidence (Table 5). Similarly, there were about 0.48, 0.42, 0.57, 0.32, 0.62, and 0.39 times lower probability that codling moth incidence would exceed >40% while apple farms were cultivated during off-season and found at an altitude of <2500 m a.s.l., recently planted trees (≤5 years), at fruit development growth stage, low levels of weed infestation, and composting and pruning for tree management in that order compared with highly risky variables in their counterpart variable classes referenced. However, 2021 year and intercrops with legumes demonstrated 2.20 and 3.57 times greater (>40%) probability of association with high codling moth incidence than 2022 year and intercrops with Irish potato (Table 6). On the other hand, mealybug incidence >20% exhibited the insect pest was risked with apple fields that cultivated in 2021 year with main rainy season, sole cropped, high weed infestation, and no tree management applied, which was 2.04, 3.34, 2.02, 3.43, and 2.03 higher than cultivation during the 2022 year, off season production, intercrops with Irish potato, low weed infestation, and tree management via composting and pruning. However, other independent variables, such as recently planted tree (≤5 years) and flowering growth stage, were comparatively less risky related to the aforementioned variables for mealybug incidence (Table 7).

The current survey investigation, together with analyses using a logistic regression model, has found biophysical and temporal factors that are highly significant and associated with the spates of woolly apple aphids, codling moths, and mealybugs. The model revealed that these factors played either a role in increasing or embarrassing the incidences of the studied insect pests. Interestingly, there were some independent variables that were more significant for enhancing the insect pest establishment than other independent variables (Tables 5–7). The model also quantified the importance of the multiple independent variables that showed how much the woolly apple aphids, codling moth, and mealybug incidences increased or decreased, suggesting that the three insect's progressive infestation was the function of those independent variables.

The overall findings of the current survey study indicated that woolly apple aphids, codling moth, and mealybug incidence vary among the biophysical and temporal factors, as explained by various degrees of incidences (Tables 2-4), and the levels of risks contributed by each of these factors against each of the insect pests in the logistic regression model analyses (Tables 5–7), although some independent variables were confounded by the influence of other independent variables that are indispensable to the studied insect pest spade development or reduction (Table 5). The use of such a model can easily be applied in a survey study to produce both quantitative and qualitative data from diverse biophysical factors over years as well as seasons to point out the epidemic risk factors. The results of an earlier survey study also suggested that by estimating the relationship between insect intensity and independent variables and identifying the most important risk factors that could either increase or decrease the development of pest outbreaks, such a model could be used to prioritize research quarries and management options (Terefe & Gudero, 2019; Mengesha *et al*., 2021). Thus, designing sustainable management strategies for the insect pests under study or others requires an understanding of how biophysical and temporal factors influence their population dynamics and intensities.

Conclusion

It was concluded that woolly apple aphids, codling moths, and mealybugs are widely distributed, economically important, and constrain productivity of apples in the study areas, and their population dynamics are significantly influenced by biophysical and temporal factors. These phenomena were explained by the prevalence, incidences, and number of insect individuals per tree, and their relative importance varied among study areas over cropping years and seasons. The study found that the woolly apple aphids, codling moths, and mealybugs continue to be a major threat to apple production year after year and season to season, with various levels of intensity as affected by biophysical and temporal factors in the areas. Regression model analyses identified that years, seasons, altitude, age of tree, growth stages, cropping systems, weed infestation, and tree management had a high association with incidences and significantly contributed to high infestation of the studied insect pests across study areas over years and seasons. The study also deduced that apple cultivation at an altitude of ≤2500 m a.s.l. with the main rainy season with recently planted trees (≤5 years), flowering to fruit development growth stages, high weed infestation, and tree management established significant relationships with low woolly apple aphids (≤15%), codling moths (≤40%), and mealybug (≤20%) incidence and can be considered as management options to reduce the impact of the studied insects on apple productivity in the study areas and related agro-ecologies. Thus, the findings could be used to establish the basis for developing sustainable woolly apple aphids, codling moths, and mealybug management strategies, as the study had been made in different production seasons for two consecutive years. However, the results implied the need for a more comprehensive study over wide locations, years, and seasons within the year for evolving and applying integrated pest management schemes targeting hosts, insect pests, weeds, proper field husbandry practices and their interactions in impacted areas, and other similar agro-ecologies.

DECLARATIONS

Author contributions

Conceptualization: Z.F., G.G. and A.A.; Methodology: Z.F., G.G. and A.A.; Software and validation: Z.F. and G.G.; Formal analysis and investigation: Z.F., G.G. and A.A.; Resources: Z.F.; Data curation: Z.F.; Writing original draft preparation: Z.F. and G.G.; Writing review and editing: Z.F., G.G. and A.A.; Visualization: G.G. and A.A.; Supervision: Z.F.; Project administration: Z.F., G.G. and A.A.; Funding acquisition: Z.F., G.G. and A.A. The authors have read and agreed to the published final version of the manuscript.

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