Diversity and functional roles of arthropod fauna across agricultural landscapes, Nilgiri Biosphere Reserve, Western Ghats, India

Author: Dr Manju Vasudevan Sharma
Conservation Team,
Keystone Foundation, Kotagiri,
The Nilgiris, Tamil Nadu, India

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INTRODUCTION

The diverse species of arthropods in forests offer a range of ecosystem services to non-forest land use categories such as agricultural landscapes. The study aimed to determine the pollinators and arthropod functional guilds in a subsistence agriculture setting in the Nilgiri Biosphere Reserve, Western Ghats, India. While large tracts of forests were converted to tea and monoculture, the approach to agriculture within the indigenous communities has been fundamentally ecological. The non-indigenous methods of farming are often chemical in the Nilgiris, except for a handful of organic private estates of coffee and tea. This offered the potential of comparing data sets from fields of natural farming and those with intensive chemical farming, expecting a higher diversity in natural farms.

In the first phase of the study, information was gathered through field studies on the pollination ecology in two economically valuable crops – coffee and mustard, along with information on natural pest control and litter decomposition in natural and chemical farms, with an assumption that chemical farming practice probably has a negative impact on abundance and diversity of invertebrate species in the various functional guilds. The approach involved community participation at all stages of research – from site selection to insect sampling to sharing of research outputs. It was hoped that the study would reinforce some fundamental concerns of chemical farming with the backing of field data on the role of diverse arthropods on pollination, pest control and litter decomposers – all crucial for the sustenance of agricultural lands.

SITES

Mustard farms in Tadsalatti village in Hasanur (N 11° 35' 45.15'', E 77° 06' 35.07'', 1222m) are organically grown. Pollination studies were carried out in this site with no comparisons with chemical farms.

Coffee plantations near wet and dry forests were sampled under chemical and organic treatments. Near wet forest type, we selected Keelkotagiri or Aracode estate (N 11° 44' 67.6'', E 76° 98'67.2'')
and Glenburn estate in Mamaram (N 11° 37' 27.8'', E 76° 92'30.3'') as chemically farmed sites and selected Keelkoop (N 11° 44' 30.0'', E 76° 98' 33.0'') villages as organic sites. Near dry forest type, we sampled in Maravala (N 11° 49'797'', E 76° 84'95.1'') and Walwood (N 11° 33'31.0'', E 76° 82' 61.9'') estates in the chemically farmed category and in Palaniyappa estate (N 11° 25' 20.3'', E 76° 73' 37.4'') and Samagudar village (N 11° 26' 27.7'', E 76° 59' 59.4'') in the organic category (see map). The sampling was carried out during the months of August-December.

Map 1: The eight coffee growing sites chosen for the study, Nilgiri Biosphere Reserve, Western Ghats, India
SAMPLING PROTOCOL

In an organic mustard farm in a village close to the forests of northern NBR, pollinator observations were made during the flowering peak. Floral visitors were monitored from 06.00 h (starting at flower opening) to 18.00 h for 30 min in each hour for 3 days, covering a randomly selected sub-site on each day. For statistical analyses, the data from the 3 days were pooled and the observation period was divided into hourly intervals. A sample of foraging insects was collected using a sweep net, and immobilized by transferring them to a vial containing a piece of filter paper dipped in ethyl acetate. The immobilized insects were observed under a stereomicroscope to check for pollen load on their bodies.

During the flowering period of coffee, which was delayed this year due to delayed summer rains in the region, malaise traps and pan traps were set up in four of the eight sites, one representing each category of forest type and agricultural treatment type. Samples from this collection are yet to be identified and what is presented in this report is the findings from pollinator observations in one chemical and one organic farm each. The lack of replicates in this study is a limitation but the narrow flowering period of coffee (3 days) combined with distances between the selected coffee sites did not allow further observations.

As explained in the site selection above, in the coffee study, there were four categories with two replicates each. In each site, we set up traps for three consecutive days during the fruiting period. We used one Malaise trap, 10 pit fall traps, 5 yellow pan traps and 5 blue pan traps. The Malaise trap was erected each morning at 07:00 h and retrieved in the evening 18:00 h. The pit fall traps (with a 10 cm diameter opening) were left in the site from 7:30 h on day one to 17:30 h on day three. The pan traps were placed randomly for 2 hours in the morning and 2 hours in the afternoon.
Fig 1 (Clockwise from top)

- Fig 1A. Yellow and blue pan traps are used for attracting flying insects. With a little soap water, they can be placed on the ground or hung to a branch of tree.

- Fig 1B. Malaise traps are like an open-sided tent with a central vertical panel which reaches down to the ground. Fast-flying insects, such as flies and wasps, hit the central panel and fly upwards towards a sloping roof that directs them towards a collecting chamber at the high end of the trap. The trap has a preservative such as ethanol in it.

- Fig 1C. Ground dwelling insects fall into pit fall traps which are placed into the earth with soap water mixed with 40% alcohol.

All specimens that were sorted were identified to Order level. Specimens identified to Family and morpho species level were fewer and composed only a small subset of the larger sample. This was
composed of 2 Malaise samples from chemical and 3 from organic sites, 2 pitfall samples from two chemical and two organic sites, 6 pan traps from chemical sites and 19 from organic sites. Insect identification work is time consuming and is still in progress at the collaborator’s lab, and when complete, a new report will be presented.

Family level identifications were carried out using Triplehorn and Johnson (2004) and Insects of Australia (1991). Identified arthropods were assigned to rough functional guilds based on their families and feeding habit.

For the purpose of analyses, we pooled the data from the 3 kinds of traps within each site. Due to the sampling strength difference in the subset of insects that were identified, pan trap results were not used for some of the analyses: specific mention of this is made in the findings section to avoid confusion. Rarefaction was an option to deal with sampling bias, but it was not done since there is in real sampling strength difference and when all insects sampled during the study are identified, then this problem will be solved naturally.

Wet and dry forest samples were also clubbed for the diversity analyses and organic and chemical farming practice comparisons. This was done since there were no apparent vegetation differences between the sites sampled. Also, in the small sub-set that was sampled here, pooling wet and dry forest data under chemical and organic types allowed the leverage of replication in the analysis. Even so, in the statistical test to look at community similarities, data from wet and dry forests were segregated.

Insects were categorised into four distinct guilds and one overlapping guild - Parasitoid, Predator, Decomposer, Pollinator, Decomposer/Predator. To examine the effect of chemical farming on arthropod richness and abundance, we conducted a Mann Whitney test. The Bray-Curtis similarity coefficient (Bray and Curtis 1957) was employed to quantify and compare the similarity of community composition among treatment types.
STUDY FINDINGS

POLLINATORS IN MUSTARD AND COFFEE

Pollination system in an organic mustard farm

Mustard is grown in the warmer climes of northern Nilgiri Biosphere Reserve. It is the crop that is sown just before beans and millets. The original objective was to compare insect functional guilds in such vegetable farms under chemical and organic farming practices. Only organic mustard sites were spotted in the region surveyed and the pan and pit fall trap insects are yet to be sorted and identified and data to be analysed.

Fig 2A. Total no. of insect visits across the day in Site A, organic mustard farm, Hasanur, northern NBR, India

Fig 2B. Total no. of insect visits across the day in Site B, organic mustard farm, Hasanur, norther NBR, India
525 visits were recorded in Site A and 884 visits in site B during the same time frame. There also appeared to be more *Apis cerana* and more *Apis florea* visits on mustard flowers in site B. The peak visitation time period was between 8 am and 11 am.

**Hedge plants**

An inventory of hedge plants was carried out in the two plots to ask if pollinator density was affected by a reduction in hedge diversity.

In site one, the hedge species recorded were - *Lantana camara, Tridax procumbens, Mimosa pudica, Euphorbia heterophylla, Leucas aspera, Sida acuta, Sida cordifolia, Euphorbia hirta, Solanum indica, Ocimum americanum and Richardia scabra.*

In site two, 15 species were recorded in the hedge: *Lantana camara, Tridax procumbens, Parthenium sp., Vernonia cenera, Amaranthus sp., Sida acuta, Citrus, Ocimum americanum, Solanum nigrum, Solanum torvum, Mirabilis jalapa, Chromolena odoratum, Richardia scabra, Lonicera japonica, Asclepias physocarpa.*

A look at the hedge diversity in these two sites suggested that pollinator abundance is directly proportional to hedge species richness. In Site A 11 species were recorded, and 15 species in site B.

An ANOVA was performed to determine if the number of visits of the different pollinators were significantly different as an influence of hedge species richness. The test showed a slightly significant difference of *A. florea* visits (p=0.0376) and a further lesser but significant difference in the visits of Ceratina (0.08) and the Dipteran (0.038).

Although this data is limited and an ideal comparison would be between at least four sites with varying hedge species richness, the analysis suggested some effect of hedge species on pollinator foraging – higher diversity of hedge species often meant more foraging resources for the pollinators (also see figure below).
Fig 3. Common hedge plants around the mustard fields in Hasanur study site. Clockwise from top left: *Asclepias physocarpa, Mimosa pudica, Richardia scabra* and *Lonicera japonica*. Photo credit: Bhagyasree VR

Fig 4. Mean no. of pollinator foraging across the two mustard sites with varying hedge species richness.
Pollination system in Coffee

In depth studies to understand the contribution of bees in coffee pollinations are few from the region (Krishnan and Ghazoul, 2012). The mid-elevation evergreen and semi-evergreen forests of NBR are coffee growing areas and chiefly two species are common in the Estates as well as small holdings of indigenous farmers – *Coffea arabica* and *Coffea robusta*. During the flowering season in April, insect visitation observations were carried out in two coffee holdings – the Aracode estate (chemical treatment) and Samegudar village (organic treatment).

![Fig 5. Apis dorsata (L) and Apis florea (R) foraging on coffee bloom, Coffea arabica holding, Nilgiri Biosphere Reserve.](image)

![Fig 6. Pollinator visitation pattern in chemical vs organic coffee farms, Nilgiri Biosphere Reserve](image)
Visitation pattern

Apis dorsata, Apis cerana, Apis florea, Trigona sp. and flies were recorded in chemical as well as organic farms of coffee. Apis florea visits were higher in the organic site of Samegudar, in comparison to the chemical site. Amegilla and Ceratina bees were not encountered in the insect visitation study in the chemical site of Aracode estate. An ANOVA was performed to determine if the number of visits of the different pollinators were significantly different as an influence of the farming practice. The test showed a slightly significant difference of Ceratina visits (p=0.032) and a further lesser but significant difference in the visits of Amegilla sp. (p=0.064) and Apis florea (p=0.07).

The bee landscape

Apis dorsata is known to have a foraging range of over 20km but visits flowers within 1 to 4 km of the nest (Dyer and Seeley 1994). They also prefer to nest on tall trees or cliffs, often located within remnant forests and not within the coffee estates (Krishnan and Ghazoul, 2012). Apis cerana and Trigona sp. seem to have more restricted foraging ranges — of about 2 km from their nests. The fact that these three species were found in comparable frequencies in the two sites is an indicator of the healthy nesting sites present in the close vicinity of the coffee holding. Amegilla sp. (blue banded bees) and Ceratina sp. (small carpenter bees) were not encountered in the chemically farmed coffee estate. These are solitary bees that nest in clay and bamboo cavities, hollow stems, old thatched roofs, or sometimes the ground. It appears that such habitats are present in the indigenous coffee growing settlements where the study’s organic site was selected.
TRAPS AND THE INSECTS CAPTURED

In Malaise traps laid across the coffee sites, a large diversity of flying insects were captured from the Orders Hymenoptera and Diptera. Several parasitoid and predatory Hymenopterans emerged in Malaise traps more than the pan traps. Very few bees made it to the pan traps in this study.

Pit fall traps gave an estimate of ground dwelling arthropods, a large number of which are detritivores. The samples were dominated by beetles, ants and spiders. In all the chemical farms that were sampled, fertilizers were used in the soil. Soils in organic farms were free of chemical application of any kind. The organic litter depth estimates revealed that in chemical farms the average depth was 1.2 inches and in organic farms the average litter depth was 2.3 inches.

SPECIES RICHNESS AND ABUNDANCE

On analysing samples from two chemical and two organic sites, from all three traps, 340 individuals were found in chemical and 796 in organic sites. When results from pan traps were not pooled in the data (since pan traps from organic and chemical sites were not comparable in the sub-sample strength), the number of individuals in chemical and organic sites were 225 and 402 respectively. No significant difference was observed in arthropod species richness and abundance of organic vs chemical sites (p=0.12, Mann Whitney Test).

Fig 7A. Mean species richness and abundance in organic vs. chemically treated coffee farms
Fig 7B. Data pooled from malaise and pitfall traps alone for the same comparison.

DIVERSITY

Diversity indices were calculated ( EstimateS 8 ) for the four sites but with data from Malaise and pitfall traps alone. The pan trap data would be used when we have comparable samples identified from chemical and organic farms. Surprisingly, the diversity index for chemical farms was higher than that for organic farms in both forest types tested.

<table>
<thead>
<tr>
<th></th>
<th>Chemical</th>
<th>Organic</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Near wet forest</strong></td>
<td>Shannon diversity index: 3.81</td>
<td>Shannon diversity index: 3.73</td>
</tr>
<tr>
<td></td>
<td>Fisher’s alpha: 50.34</td>
<td>Fisher’s alpha: 45.92</td>
</tr>
<tr>
<td><strong>Near dry forest</strong></td>
<td>Shannon diversity index: 3.97</td>
<td>Shannon diversity index: 3.27</td>
</tr>
<tr>
<td></td>
<td>Fisher’s alpha: 63.53</td>
<td>Fisher’s alpha: 30.37</td>
</tr>
</tbody>
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This might have to do with the evenness of species distribution in these sites. A comprehensive picture would emerge only after samples from all 8 sites are identified and fed into the various analysis tools. Before the complete analyses, it would be inappropriate to make a conclusive remark.
VARIATION IN FEEDING HABITS

The mouth parts of insects determine their functional role in an ecosystem. Most Homopterans and Diptera are herbivores with sucking and piercing mouth parts, allowing them to feed on sap, and thus some of them are crop pests. Thysanoptera (thrips) are also fluid feeders as larvae and adults. Adult Hymenopera have biting and chewing mouth parts, but bees are nectar-feeders and are described as lapping nectar. Larval Lepidoptera and Coleoptera have well-developed biting and chewing mouth parts.

FUNCTIONAL GUILDS

Herbivores or pests

Several beetles such as the ones under Family Scolytidae are borers and important pests. Other phytophagous insects such as Coleoptera (beetles) are herbivores and so are many species of crickets and ants.

Natural enemies: Parasitoids and Predators

A large number of the Hymenoptera in the study were either parasitoids that parasitise pests or predators that prey upon pests. Wasps of Scelionidae, Braconidae, Chalcididae and Eupelmidae, for instance, are beneficial groups of parasitic Hymenoptera since they are considered good pest control agents, since they parasitise eggs and adults of several insect Orders. Aphelinidae in particular are parasites that attack Hemiptera and are used as biocontrol agents. Hymenopteran predators are from Families such as Vespidae, Pompilidae, Sphecidae and Diapriidae.
Some Dipterans are predators – Dolichopodidae and Acroceridae are good examples. Cecidomyidae are gall makers but predate on small insects like Aphids, which are common pests. Pit falls from organic sites recorded several individuals of the Order Collembola that are a common predator group too.

Carabid beetles (Coleoptera), which did not emerge in our current sub sample set, are important predators of many invertebrates, including agricultural pests like snails. They are common in more arid habitats.

Spiders are an ecologically important arthropod Order and they were the other dominant predator group found in this study.

Jumping spiders (Fam: Salticidae) are predators in many habitats (L). The Ichneumoinid wasp belongs to a large group of parasitoids (R).

**Decomposers**

This category included a diversity of litter fauna: detritivores such as ants (Formicidae), and a whole range of fungal feeders. Dark winged fungus gnats of family Sciaridae, and species of Mycetophilidae and Drosophilidae (all Diptera) live in decaying vegetation and fungi. Coleopterans of family Nitidulidae and Scarabaeidae are also excellent decomposers. The larvae of Lauxaniidae live in decaying vegetation; in this study they were recorded only in the organic coffee sites. Although thrips are good pollinators of canopy trees, we classify them under decomposers since adults are fungal feeders too.
A thrip (Phlaeothripidae) emerges out of a canopy flower (L). Scavenger flies feed on carrion and inhabit moist terrestrial habitats (R).

**Functional guild overlap**

The kind of overlap of ecological functions seen in thrips is not uncommon among arthropod groups. Thrip larvae in fact mine into leaves, so that makes them not just decomposers and pollinators, but also herbivores. Members of many other families such as Scolydae, Tiphidae, Spahecidae, Vespidae and Pompilidae are predators but frequently visit flowers for nectar. They would feature in a guild overlap of pollinator/predator but there were few representatives.

Some beetles such as Staphylinids and Psocopterans such as Trogiidae are seen in decaying material, fungi and leaf litter, some are parasites and predators of other insects. Therefore in this study they are classified under the overlapping functional guild of Decomposer/Predator. Similarly Formicidae (ants) combine the role of herbivore and carnivore but a large number of them are detritivores. Therefore they are also classified under the Decomposer/Predator overlap guild.

Ants (Fam: Formicidae) are good predators and detritivores too.
**Pollinators**

The pollinator guild was composed of fig wasps (Agaonidae), Halictid bees and Mordellidae (flies) (Fig 8). What may be noted here though, is that the pollinator guild appears depauperate not only because the sample subset analysed here is largely from the non-flowering season, but also because we had almost no bees captured in Malaise and pan traps. The observations during the flowering period of coffee are not listed in the classification table below.

**ORGANIC VS CHEMICAL – Functional Guild Composition**

One of the pressing questions was to know if there was a difference in the functional guild composition associated with chemical or organic farming practices. Once the identified insects were classified into the five functional guilds, all it took was a simple graph. In the entire data set, natural enemies formed the largest group, followed by decomposers. Species richness values of arthropods from all functional guilds were higher in organic sites as compared to chemical sites.

![Fig 8. Species richness in organic vs chemical coffee farms as segregated under the five functional guild categories.](image-url)
### Table 1. The arthropod assemblage captured in the study as classified under the functional guilds

The number of species of each Family under all guilds is presented in parenthesis. This list is from four sites out of the eight sampled. A larger list is likely to emerge when the insect identifications are completed.
SIMILARITY IN COMMUNITY COMPOSITION

We used the Bray-Curtis similarity coefficient (Bray and Curtis 1957) in EstimateS 8 to quantify and compare the similarity of community composition among treatment types. When the entire data set was used (including pan trap results), the Bray–Curtis similarity coefficient between chemical and organic coffee sites was 26.2% (Fig 9A) and the Sørensen index of similarity was 35.8%.

Fig 9A. Cluster diagram depicting the Bray-Curtis similarity index between chemical and organic farm samples from all the 3 trap types pooled in.

Estimates 8 was used to carry out insect community assemblages comparisons between wet and dry forest types within chemical and organic farms, with results from malaise and pitfall traps alone. Chemical and organic farms of wet forest types (Chem 1 and Org 1 in Fig 9B) had more similarity (Bray-Curtis of 19.8% and Sørensen 25.5%) than two organic sites (Bray-Curtis 0.5% and Sørensen 14.3%). The similarity index of chemical and organic farms of dry forest type (Chem 2 and Org 2) was also higher (Bray-Curtis 18.3% and Sørensen 22.5%) than that between two organic or two chemical sites. This suggests that unlike what was expected from apparent vegetational similarities, insect communities do assemble across wet and dry forest types as distinct microhabitats. Forest
type appears to be a determinant of community structure, and the differences in farming methods only influence or alter the existing diversity within the particular forest type. Another very crucial lead from this is that the least similarity between organic and chemical sites in fact may indicate that the community composition undergoes a shift as an influence of the farming practice. Other analyses (presented earlier) also suggest that chemical farming reduces the diversity and abundance of invertebrates.

Fig. 9 B. Cluster analysis diagram for the Bray-Curtis similarity index test, representing a similarity of 19.8% between chemical and organic farms of wet forest type (lower branch) and 18.3% between chemical and organic farms of dry forest type.
DISCUSSION

Invertebrates are functionally essential in a diversity of landscapes, particularly in the tropics. An impression of our ignorance of tropical forest insects can be gauged by looking at the proportion of species that cannot be named from each of a number of taxa (Ghazoul and Sheil). Still less is known of the ecology of invertebrates.

In the Western Ghats of India, considered a biodiversity hotspot, land use change has negatively impacted biodiversity in the past few decades. Even so, indigenous communities living close to forested landscapes have retained much of the original diversity around them without exploiting the resources available. Some communities have also been farming as one of the livelihood sources—traditionally they have grown millets and vegetables, but ever since plantations came to the hills, they have also kept small holdings of coffee. The current study which was conceived to detect changes in arthropod biodiversity across chemical and organic farms was also conducted in some of these indigenous farms in the Nilgiri Biosphere Reserve. Although only a small fraction of the entire collection of arthropods was identified and used in data analysis, it gives the impression that organic farms do support a higher number of species and a higher diversity of functional guilds in comparison to chemically grown farms. In all the five categories of functional guilds, species richness and abundance of arthropods were higher in organic coffee farms as against chemical coffee farms. The analyses on community structure and similarity between organic and chemical farms across wet and dry forest types suggests that there is least similarity between organic and chemical sites, even within a geographically similar landscape. In fact, wet sites and dry sites had more similarity than chemical and organic sites. This might imply that the arthropod composition undergoes a community shift as an influence of chemical farming.

Biodiversity in semi-natural or human dominated habitats is as important to be conserved as is in wilderness areas such as forests. Protecting the existing diversity in agricultural landscapes close to forest areas is crucial especially in terms of bees and birds that forage in such systems, and for a range of arthropods that have specific roles to play in maintaining the ecological harmony of the habitat. Insects are usually associated with crop damage, while only a small fraction of the world’s insect population comprises pests. A far larger number of them are beneficial in more ways than one. Recent approaches to crop management have incorporated practices of Intergrated Pest
Management which involves the principle of ‘managing’ insects, in contrast to eradicating them, so that populations remain below a particular threshold level. Farmers can in fact benefit from incorporating beneficial techniques to attract insects (and birds) to assist with pest control and increase pollination efficiency. In the insect functional guilds guide developed as part of this project, and which is being distributed to the indigenous farmers network and the bigger estates, the following are the recommendations made:

- Maintain high hedge diversity – they are great foraging sources for pollinators and home range for spiders.
- Keep the crop free of pesticides during flowering – bees would be safer.
- Retain large native trees since social bees prefer making their hives on them.
- Maintain old bamboo and cane roof panels, mud banks and clay surfaces: these are excellent nesting sites for solitary bees.
- Provide for bird and spider habitats - they can help control borers and miners that are pests.
- Leave leaf litter on the crop floor – the insects in there only make your soil nutrient rich.

These are some of the ways to enhance the presence of pollinators, predators of pests and detritivores in an agro-forest landscape.

One such effort in the Nilgiris as an initiative of Keystone’s beekeeping training group was to set up reeds in small cut bunches to provide additional nesting sites for solitary bees. By refraining from spraying pesticides, a farmer could assure healthy populations of natural enemies of pests, and by avoiding the use of fertilizers, decomposers would thrive on his land. Other insect friendly practices involve maintaining hedge diversity, promoting mixed cropping systems, and retaining large trees and natural surfaces such as clay and dead wood or bamboo to support bee nesting. Several estates in the region are now part of the Rainforest Alliance and are keeping a record of biodiversity on
their land. Estates that are organic are also planting native trees to be able to replace the old stands of Silver Oak.

These ecological incentives could be combined with economic incentives by assuring organic farmers of a fair price through systems such as the Participatory Guarantee System that exists in Keystone’s partner farming villages in the region. Keystone encourages agricultural communities to manage and control the production and marketing of economically valuable organic crops such as millets, vegetables and coffee. Since the fundamental thrust is on agro-biodiversity, there is a need to develop more such community involved studies that help understand the trends in biodiversity in natural as well as human modified landscapes of the region.

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REFERENCES

   Ecological Monographs 27:325-349.