Tropical agroecosystem functions in a changing environment

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Tropical agroecosystem functions in a changing environment.

Abstract

In many tropical regions, forests have been extensively converted to various land uses, notably through the expansion of agriculture. Both biodiversity and associated ecosystem functions and services have been eroded in these human-modified tropical landscapes. My research investigates the effects of land-use change on invertebrate communities and ecosystem functioning from both fundamental and applied ecological perspectives, as well as the risks posed by global environmental change, mainly agriculture and climate change in tropical ecosystems. I focus on a human-modified tropical forest landscape associated with Panua Nature Reserve in Sulawesi, Indonesia. Despite its protected status, Panua Nature Reserve has seen extensive human disturbance, resulting in a mixture of forest, shrubland, and maize fields within the reserve. My study area is a tropical landscape shaped by small-scale farming. Small-holder farmers constitute the majority of tropical farmers and are severely marginalised.

I used a field experiment to evaluate the effects of habitat modification on decomposition, and explored how decomposition varied with substrate type and composition of the decomposer community (Chapter 2). By exposing leaf litters within litterbags and toilet rolls in the above-mentioned habitat types, I found that litter and cellulose decomposition differed across habitat types with highest decomposition was in the forest sites. The results suggest that even small-scale agriculture can reduce the decomposition of organic materials.

Using plasticine caterpillars (Chapter 3), I investigated predation by potential predator groups to determine the effect of habitat modifications caused by maize farms on predation, and to test whether predation of herbivorous insects is forest-dependent. Predation was significantly reduced in the most modified habitat, maize fields. In addition, predation of caterpillars is forest dependent, indicated by spillover from forest habitats to the maize farms. Similar to the results of the Chapter 2, the results of this chapter suggest that small-scale agriculture alters predation of herbivorous insects, and that predation of caterpillars in maize farms relies on the predator from nearby natural habitats.

In Chapter 4, I report a field mesocosm experiment to evaluate ecosystem functioning of the litter invertebrate community in response to simulated environmental change by manipulating (1) community composition (millipedes and other litter invertebrates), (2) soil moisture levels (dry, ambient, and wet) to represent extreme precipitation conditions, and (3) two distinct land uses (shaded and open areas representing the forest and agricultural land, respectively). The results highlight the importance of millipedes among invertebrate decomposers in maintaining decomposition in a changing soil environment.

Lastly (Chapter 5), I determined forest fragments' functional contribution to maize farmland by quantifying predation of caterpillars and cellulose degradation over six transects across forest and maize farmland. I found that ecosystem functions differed in the extent to which forested areas contributed to functions in adjacent farming. In this instance, predation of caterpillars was influenced by proximity to forest, but decomposition was not. This suggests that ecosystem functions have different dependencies on natural habitats.

In general, this thesis reveals that degradation of Sulawesi's forests causes a decline in ecosystem function. In the forest habitat, decomposition rates, insect predation rates, and pest control services were all considerably higher than in degraded habitats. Millipedes (Diplopoda) were found to be a noticeable and numerically dominant component of the macroinvertebrate community and have a major positive effect on nutrient recycling. To better understand the contribution of this under-studied taxon to ecosystem functionality in a changing environment, more research is needed to investigate how invertebrate communities in the agroecosystem landscape affect decomposition and soil nutrient input in different habitats and under altered climatic conditions.

This thesis findings suggest some practical implications in conservation. Despite often perceived negatively by public, invertebrates need to be conserved because of their important roles in the ecosystems. Discovering invertebrate biodiversity and understanding their benefits for the farmers are some of the keys in supporting invertebrate conservation. In the landscape level, sustainable agriculture practices, such as forest strip establishment and soil mulching in agricultural land, could potentially conserve invertebrates while maintaining agriculture production.

Format of Chapters

This thesis is in an integrated format where each of six chapters represents a separate journal articles. All of them have been submitted for publication, of which 1 article has been made available as preprint. The details of the journals are:

Chapter 1: General Introduction

Chapter 2: Ecology and Evolution – in review, available on Biorxiv

Chapter 3: Journal of Tropical Ecology- in review

Chapter 4: Biotropica - in review

Chapter 5: In preparation for submission.

Chapter 6: General Discussion

Apart from the thesis chapters, the Appendices contain three additional papers finalised during the duration of my DPhil time (two published, three under review, and two under preparation) either as first-author or co-author. Parts of this thesis have also been presented at the Association for Tropical Biology and Conservation (ATBC) Annual Meeting 2021, the International Congress for Conservation Biology (ICCB) 2021, and the INTECOL Symposium 2022.

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Chapter 1: General Introduction

Tropical forests and their challenges

Tropical forests are home to the highest organismal diversity on Earth, and South-east Asia is a particular hotspot for biodiversity. However, the region is currently experiencing some of the highest deforestation rates ever recorded (Miettinen et al., 2011), which significantly contributes to the loss of biodiversity worldwide (Sodhi et al., 2010). Not just in unprotected forest, but also in biologically significant protected areas, forest loss is taking place. Despite being the main strategy to conserve natural resources and reduce biodiversity loss (Jepson et al., 2017), many protected areas in tropical region receive severe disturbances from forest fires (Juárez-Orozco et al., 2017), logging (Fredericksen & Peña-Claros, 2007), mining (Wantzen & Mol, 2013), and agricultural conversion (Reyes et al., 2010). Rapid human population growth has heightened the risk of disruptions to ecological processes (biological, chemical, and physical) that support ecosystem integrity (Brockerhoff et al., 2017).

Although majority of the biodiversity and associated ecosystem functions, carbon, climatic, and soil-hydrological services (Edwards et al., 2014), as well as conservation values (Berry et al., 2010), have largely been preserved in tropical forests, selective logging and new investments for logging activities are foreseen to cause more harm than good (Bowles et al., 1998). The demand for wood for construction has led to direct timber harvesting from tropical forests, which could dramatically lower the forest biomass over time (Cazzolla Gatti et al., 2015) and change the production and allocation of carbon (Riutta et al., 2018). Logging in tropical forests significantly disturbs the below-ground carbon balance in addition to having an impact on above-ground carbon dynamics (Riutta et al., 2021). Up to 12% of the total carbon emissions brought on by deforestation are attributable to tropical forest logging (Pearson et al., 2014).

Tropical forests and changing land-use

Between 1980 and 2000, more than 55% of new tropical agricultural land came from conversion of primary forests, and another 28% came from disturbed forests (Gibbs et al., 2010). The rapid growth of agriculture, which is motivated by the increasing demand for agricultural commodities, is frequently followed by logging and farm expansion to fulfil the demand, which keeps reducing forest cover (Newton et al., 2013). In other cases, agricultural expansion is started with forest logging that reduces forest quality, thus detaching the protection status of the forest. With the conversion of about 6 million hectares of tropical forests for agricultural use (Carrasco et al., 2017; Gibbs et al., 2010), agricultural intensification and

expansion pose a serious risk to tropical forests (Mayaux et al., 2005). Likewise, the ecosystem functions that rainforest biodiversity provide (Lewis, 2009), such as pest control and soil fertility, are diminished when forests are converted to agricultural land (Holle & Lewis, 2022 (Chapter 2); Chapter 3).

On a smaller scale, human disturbances suppress tropical forests and have edge effects that have an impact on species assemblages as well as ecological processes (Foggo et al., 2001). Edge effects are a significant driving factor that can disrupt food webs, nutrient cycles, and ecosystem functioning because of the physical and biological alterations that arise (Foster & Bhatti, 2006; Laurance et al., 2007; Morris, 2010). However, there is little research on how ecosystem functions respond to edge effects (Riutta et al., 2016), especially in tropical forests (Brandon, 2014; Morris, 2010).

Tropical forests and changing climate

Climate change is expected to have significant effects on tropical ecosystems, along with deforestation and ecological degradation. Unquestionably, tropical forests are important to the water and carbon cycles on Earth (Bonal et al., 2016; Corlett, 2016), yet some tropical forests are projected to experience changes in precipitation patterns that could reduce carbon uptake and cause forest dieback. Human disturbances that affect the capacity of forests to mitigate climate change, such as wildlife hunting, forest fires, and deforestation will continue to disrupt climate condition (Deb et al., 2018; Holm et al., 2017). The impacts of human-induced climate change on drought event frequency and intensity could weaken the tropical forest carbon sink, with resulting feedback to future climates (Corlett, 2016).

Climate variability and changes in tropical Asia are increasing air temperatures and altering precipitation patterns (Bonal et al., 2016). In Southeast Asia, which is now experiencing some of the world's highest deforestation rates (Miettinen et al., 2011), regional and seasonal climate variability and trends vary substantially (IPCC, 2014). Drought dominates the dynamics of tropical rainforests, and the response mechanisms are extraordinarily diverse and complex (Bonal et al., 2016). Drought frequently causes tree death in the forest, resulting in canopy gaps and a surge in the decomposition of organic matter from dead trees on the forest floor. Therefore, the response of ground-dwelling invertebrates to the direct (e.g., elevated temperature, decreased precipitation) and indirect (increased dead organic matter) effects of climate change has significant implications for ecosystem services such as decomposition, nutrient cycling, and soil structure regulation (Perry & Herms, 2017). Moreover, climate change and disturbance can result in a long-term decline in biodiversity and associated

ecological services (Kagezi et al., 2016). However, the effects of complex community interactions and ecosystem services, as well as climate change, on less charismatic taxa, such as certain invertebrates and fungi, are overlooked and hence pose significant research gaps (Brockerhoff et al., 2017).

Agriculture as the major challenge

Among the many issues tropical environments face, agriculture has become one of the most significant contributors to deforestation and greenhouse gas emissions, which could exacerbate the climate catastrophe. Researchers and practitioners have sought to mitigate the adverse effects of some tropical crops, including oil palm, coffee, and cacao which are widely grown in southeast Asia. Much of this work has taken place on large-scale, industrial or company-owned farmland. Meanwhile, there are over 500 billion smallholder farms in the world, most of which are in tropical regions and low- and middle-income nations (Ricciardi et al., 2021). These small holder farmers are vulnerable to significant crop failures, food insecurity, and income loss when disturbances occur (Rakotobe et al., 2016), which intensifies the complexity of sustaining tropical agriculture, which frequently involves a trade-off between profit and environmental impacts. In vulnerable circumstance, small-scale farmers may prioritise profit over environmental preservation, so perpetuating the damage.

One of the challenges that frequently prevents farmers from implementing sustainable agriculture is crop failure. Common causes of crop failure include infertile soil and pest infestation. When crop failure leads financially sensitive small-holder farmers to lose income, they will minimise the loss through land expansion and intensify the land by adding more chemicals to increase yields. In contrast, maintaining a sufficient crop yield is presumed to motivate farmers to implement sustainable agriculture, given that sustainable agriculture practises can be advantageous over business-as-usual practise (Kassie et al., 2009), thereby reducing farmers' reliance on external inputs (i.e. chemical fertilisers) and enhancing inherent soil fertility (Scholberg et al., 2010).

Some of the contributing factors to the economic loss caused by crop failures in seasonal monoculture are soil degradation and pests or weeds (Crews et al., 2018). The species-poor communities of monoculture plantations are more prone to soil fertility decline (Ewel et al., 1991). In addition, soil fertility is regulated by efficient nutrient cycling that relies on decomposition processes (Gray & Lewis, 2014; Power, 2010; W. Zhang et al., 2007) and is mediated by biodiversity (Lewis, 2009). The decomposition of organic matter, such as leaf litter and wood, is affected by climatic conditions and biotic factors, such as the activities of

decomposer communities: bacteria, fungi, and macrofauna (such as earthworms, termites, and other litter invertebrates) (Both et al., 2017; Mohan, 2017; Power, 2010).

Similarly, the absence of natural enemies of pests results in yield losses for many of the most important tropical crops (Oliveira et al., 2014). As an alternative to high-input and typically environmentally harmful pesticides, these agricultural pests can often be suppressed naturally by top-down control from predators (Zhang & Adams, 2011). Arthropods and mammals dominate insect herbivore predation in tropical agriculture (Denan et al., 2020). The biological control of pests by predators, parasitoids, and pathogens is a component of pest control services (Power, 2010; Tscharntke et al., 2005).

In considering the challenges and gaps in agroecological research, each chapter of this thesis focuses on agriculture in the specific contexts of (1) location: tropical agroecosystem landscape within and adjacent to protected areas; (2) crop types: maize as a representative of a smallholder seasonal crop; and (3) crop production issues at the study sites: soil infertility and pest outbreaks.

Agroecosystem functions

Table 1.1. Key ecosystem functions and their providers, as well as ecosystem services in agricultural land and natural habitat (Adapted and modified from Sekercioglu et al., 2010).

Ecosystem functions	Ecosystem function providers	Ecosystem services	
		In the agricultural land	In the natural habitat
Decomposition	Leaf litter and soil invertebrates, soil micro-organisms, nitrogen-fixing plants, plant and animal production of waste products.	Soil fertility maintenance, crop yield	Soil fertility for plant regeneration
Pollination	Insects, birds, mammals	Food production	Reproduction
Predator-prey interactions	Invertebrate parasitoids and predators, vertebrate predators (mammals, birds, reptiles).	Pest control service	Population control, biodiversity maintenance

Agroecosystems are the ecosystems that exist on agricultural land. Intentionally designed to cultivate crops and generate food for humans, they inevitably provide habitats for other organisms. These man-made ecosystems may supply ecosystem functions, which in this case are termed as agroecosystem functions. These ecosystem services are supported by the biodiversity that occupies agricultural land exclusively or moves between agricultural land and nearby ecosystems.

Linking ecosystem functions and the previously stated crop issues, I now elaborate on the ecosystem functions associated with soil infertility and pest outbreaks, namely decomposition and predation of herbivorous insect pests, which are the most common causes of agricultural production loss at my study site.

Soil fertility maintenance

Nutrient cycling is one of the most fundamental cycles for regulating the growth and survival of plants. In tropical ecosystems, nutrients are distributed predominantly in the vegetation and to a lesser extent in the forest floor and soil (Foster & Bhatti, 2006); consequently, the nutrient cycle in the majority of tropical forests is reliant on ecological processes such as decomposition (Yeong et al., 2016), herbivory, and predation via cascading trophic effects (Belovsky & Slade, 2000; Roels et al., 2018). These ecological processes rely on diverse animal groups, including fungi and litter invertebrates in the case of decomposition (Chellaiah & Yule, 2018; Voriskova & Baldrian, 2013) and arthropods, birds, mammals, and reptiles in the herbivore predation process (Low et al., 2014).

Due to the low nutrient availability of most tropical soils, decomposition plays a crucial role in maintaining the nutrient cycle (Yeong et al., 2016). Fungi are believed to have a significant role in litter decomposition (Chellaiah & Yule, 2018; Voriskova & Baldrian, 2013), especially when nutrients are sufficient (Pascoal & Cassio, 2004). In addition to fungi, litter invertebrates such as ants, dung beetles, termites, earthworms, millipedes and isopods play a significant role in decomposing organic matter (Burghouts et al., 1992; Leitner et al., 2018; McGlynn & Poirson, 2012) and facilitating the recovery of degraded ecosystems (Snyder & Hendrix, 2008). Decomposer community composition, that includes macrofauna, mesofauna, and microorganism, drives the decomposition process (Díaz, 2001). Therefore, the importance of fungi-invertebrate associations and interspecies interactions within the litter invertebrate community in determining their contribution to the decomposition process cannot be overstated.

In forest ecosystems, decomposition of organic matter such as leaf litter and wood is influenced by inter-related drivers, including the decomposer community, tree species diversity (which is in turn linked to substrate diversity (Joly et al., 2020; Oliveira et al., 2019)), native substrate availability (Chomel et al., 2015), and microenvironment (Hector et al., 2000; Oliveira et al., 2019). Bacteria, fungi, and macrofauna (including earthworms, termites, and other litter invertebrates) make up decomposer communities (Both et al., 2017; Mohan, 2017; Power, 2010). In general, higher humidity and temperature (Dan et al., 2016; Salinas et al.,

2011), a nutrient-rich environment (especially for fungus-mediated decomposition) (Pascoal & Cassio, 2004), and a diverse litter fauna, comprising both macro and microfauna, improve decomposition (Bradford et al., 2002; Gonzalez & Seastedt, 2001).

Pest control

Organisms at higher trophic levels play a crucial role in controlling herbivory through the process of predation (Leles et al., 2017). If insect herbivores are attacking crops, predation can also be viewed as a pest-control service; it decreases herbivore damage and boosts crop yields (Lucey & Hill, 2012; Rand et al., 2006; Rand & Louda, 2006). Considering their role in maintaining ecological processes in tropical landscapes, especially those that are highly diverse but understudied, fundamental studies of the contributions of nutrient cycling-involved focal taxa to ecosystem functions would provide valuable insight into optimising their services.

Balancing sustainability and economic of the pest control often uses the principles of the Integrated Pest Management (IPM), which integrates different practices to grow healthy crops while reducing the use of pesticides (FAO, 2023). Various biological control agents are utilised to reduce the impact of agricultural pests. For example, Babendreier et al. (2019) suggested that promoting the use of *Trichogramma* as a pest control agent needs to be further promoted for facilitating the reduction of the pesticide use. These pest control agents belong to several biological groups, including target-specific parasitoids and other predatory invertebrates or vertebrates (Sekercioglu et al., 2010; Yang et al., 2014). Abiotic factors such as temperature, atmospheric CO2, and precipitation may alter predator–prey interactions in arthropod groups (Laws, 2017; Laws & Joern, 2013).

Biological control can be seen in classical biology and conservation biology perspectives (Hessel, 2013). In the classical biology point of view, natural enemies of pests are introduced in order to lower pest abundance, which is expected to reduce the crop damage, thus economic impacts are reduced. The classical biological control programmes rely on several drivers, such as the ability of the biocontrol agents in foraging and targeting the pests, adaptability to the new environmental condition, and host range specificity (Hajek, 2004). Meanwhile, from conservation biology perspective, management of agroecosystem considers the facilitation of the action of naturally occurring natural enemies of pests (Nurdiansyah, 2016). Because most arthropod species experience their habitat at spatial scales beyond the plot level, and natural enemies spillover across the crop-non crop interface (Chapter 3), conservation biological control in agroecosystems demands a landscape management approach (Tscharntke et al., 2007).

While some studies have found limited evidence for 'spillover' of predators from forest fragments to agroecosystems (Gray & Lewis, 2014), others have shown that at least some insect taxa have elevated species richness or abundance in agricultural land adjacent to forests (Lucey & Hill, 2012; Lucey et al., 2014). Spillover effects of predation can occur bidirectionally, from natural habitats to managed land and *vice versa* (Blitzer et al., 2012). Where spillover occurs, it can nonetheless be ineffective in reducing pests (Tscharntke et al., 2016). Such effects can also vary temporally; for example predator spillover from natural habitats into nearby farmland can occur during the early stages of crop growth, but be reversed later in the season (Rand et al., 2006).

Millipedes as decomposers

The third most diverse group of terrestrial arthropods is millipedes (Diplopoda) (Kime & Golovatch, 2000). However, millipedes are among the least researched groups ecologically, with the majority of research occurring in temperate environments (Sierwald & Bond, 2007) and sparse data from tropical forests, where they reach their greatest diversity (Brewer et al., 2012). In tropical ecosystems, millipedes mostly serve as decomposers (Kumar & Shakunthala, 2016; Sierwald & Bond, 2007; Smit & Van Aarde, 2001). With their narrow tolerances and consequent rapid responses to environmental change, millipedes are sometimes used as bioindicators (Masse et al., 2017).

As decomposers, millipedes consume a wide variety of materials, particularly leaf litter (Lawrence & Samways, 2003) in tropical regions (González et al., 2012). For instance, the Seychelles giant millipede consumes around 17.19% of daily litter fall, making a major contribution to nutrient cycling (Lawrence & Samways, 2003). Despite their probable significance for soil nutrient availability, millipedes and other litter macrofauna appear to be overlooked by current landscape management policies (Contos et al., 2021). In addition, whereas the association between organismal density and decomposition rates is well-established in other decomposer systems (Gotcha et al., 2022; Klemmer et al., 2012; Little et al., 2020), little is known about how millipede density affects decomposition rates.

Outline of thesis

In this thesis, I investigate ecosystem functions provided primarily by invertebrates using an experimental approach under changing land-use (Chapters 2, 3, and 5) and climatic conditions (Chapter 4). I analysed how two major ecosystem functions, litter decomposition (Chapter 2) and predation of caterpillars (Chapter 3), vary over a gradient of habitat modification, from tropical forests to agricultural land. Focusing on litter decomposition

mediated by invertebrates, I conducted a mesocosm experiment to determine how experimental climate change and shifts in the litter invertebrate community affect decomposition and its related parameters (Chapter 4). Finally, I investigated how ecosystem functions are transferred from natural habitat to human-modified habitat (Chapter 5).

This thesis particularly addresses the following questions:

1. What are the impacts of habitat modification on decomposition and decomposer communities?
2. How does habitat modification influence predation of caterpillars?
3. How do changing precipitation and fauna community composition affect ecosystem functions?
4. Is there spillover of ecosystem functions (decomposition and predation of caterpillars) from natural habitat to nearby agricultural land?

Chapter 2: Altered litter and cellulose decomposition across an anthropogenic habitat modification gradient in Sulawesi, Indonesia

M. J. M. Holle & O. T. Lewis, *in review*, *Ecology and Evolution*

Author contribution

MJMH carried out the fieldwork, analysed the data, and wrote the manuscript. OTL provided suggestions and ideas on experimental design and commented on the manuscripts.

Abstract

Many tropical regions in Southeast Asia have experienced extensive habitat modification, creating a mosaic of forested and agricultural land. The capacity of these human-modified tropical landscapes to support biodiversity and ecosystem functions and services is of considerable practical interest. Decomposition of plant material is a key process maintaining the nutrient cycle in both natural and agroecosystems, but few studies have documented the relative contributions of different guilds of decomposers, acting on different plant substrates, across different tropical land-uses. We measured decomposition of leaf litter and cellulose across a gradient of anthropogenic habitat modification (forest, shrubland, and maize farmland) within Panua Nature Reserve, Sulawesi, Indonesia. The influence of fungi and the litter invertebrate community were investigated experimentally. Decomposition of both substrates was significantly lower in maize plantations than in forest sites. Partial exclusion of litter invertebrates, but not fungi, significantly reduced decomposition, but the feeding guild composition of the litter invertebrate community did not differ significantly across habitat types. Our results confirm that even small-scale agricultural areas adjacent to forest fragments can experience impaired ecosystem functions. These changes can be linked to reduced invertebrate activity, apparently independent of the functional structure of the litter invertebrate community. Effective management of human-modified landscapes will be needed to maintain nutrient cycling, even in areas where agroecosystems and tropical forests occur in close proximity.

Keywords: Tropical forest, Sulawesi, decomposition, substrate, fungus exclusion, and litter invertebrate community.

Introduction

Tropical forests are a global priority for conservation and restoration because of their high biodiversity and provision of multiple ecosystem services (Brandon, 2014; Mokany et al., 2014; Brancalion et al., 2019; Strassburg et al., 2020). Southeast Asia is home to nearly 15%

of the world's tropical forests (Stibig et al., 2014; Estoque et al., 2019), but has the highest annual rate of deforestation and forest degradation among tropical regions (Mayaux et al., 2005; Miettinen et al., 2011; Stibig et al., 2014). Reflecting global trends, conversion of forests to agriculture, especially oil palm and rubber, is the main cause of forest loss (Stibig et al., 2014) and the resulting biodiversity crisis (Wilcove et al., 2013) in Southeast Asia. The fate of tropical forest biodiversity strongly relies on the effective management of human-modified landscapes, including areas where agroecosystems and tropical forests occur in close proximity (Gardner et al., 2009), and on the integration of management for ecosystem functions into land-use planning (Power, 2010).

Despite being a driver of tropical deforestation, agriculture production relies on ecosystem services that tropical forest ecosystems provide, such as soil fertility regulation through decomposition processes (Zhang et al., 2007; Power, 2010; Gray & Lewis, 2014), which are mediated by rainforest biodiversity (Lewis, 2009). As agricultural expansion creates human-modified 'matrix' landscapes that now dominate most tropical regions (Brancalion et al., 2013), protecting forest remnants may be crucial to support the fertility of nearby agricultural land.

Along with plant litter productivity (Veen et al., 2019; Giweta, 2020), decomposition is an important driver of soil nutrient availability through efficient cycling, especially where soils have low fertility (Yeong et al., 2016; Grau et al., 2017). Furthermore, soil nutrients are also a limiting factor for tree seedling growth (Santiago et al., 2012). Decomposition of organic matter such as leaf litter and wood, is influenced by climatic conditions and biotic factors, such as the activities of decomposer communities: bacteria, fungi and macrofauna (including earthworms, termites and other litter invertebrates) (Power, 2010; Both et al., 2017; Mohan, 2017). In general, decomposition is promoted by higher humidity and temperature (Salinas et al., 2011; Dan et al., 2016), a nutrient-rich environment (particularly for fungus-mediated decomposition) (Pascoal & Cassio, 2004), and a rich litter fauna, including both macro and microfauna (Gonzalez & Seastedt, 2001; Bradford et al., 2002). Numerous studies provide information on decomposition processes in tropical regions, but knowledge remains incomplete on two important aspects.

First, there is uncertainty about how decomposition rates vary across land-use gradients in interaction with biotic and abiotic factors. Studies have variously reported that decomposition rates in tropical forests are influenced by climate (Powers et al., 2009), habitat quality (e.g. litter: Kagezi et al., 2016; Yeong et al., 2016, dung: Saleh, 2015), litter amount or quality (Ashford et al., 2013; Chellaiah & Yule, 2018), and the composition of the biotic

community of arthropods (Ashford et al., 2013) or microbes (Chellaiah & Yule, 2018). However, there is a lack of consistency in the reported role of these different drivers. For example, Both et al. (2017) found that land use is a stronger driver than litter quality, while Powers et al. (2009) found that climate was the main driver, not mesofauna or litter type.

Second, there is a shortage of studies documenting and comparing decomposition of different substrates. While decomposition studies using leaf litter as the substrate are common, the study of wood decay has been relatively neglected (Pietsch et al., 2019). Cellulose-rich woody material is a key organic input, and is also important for tracking carbon balance changes including those linked to logging operations (Leitner et al., 2018). A recent study has shown that invertebrates such as insects have particularly pronounced effects on dead wood decomposition under the warm, humid conditions of tropical forests, accounting for a substantial fraction of the carbon flux from dead wood (Seibold et al., 2021).

In this paper, we investigate the importance of different components of the biota (invertebrates and fungi) as agents of decomposition across a gradient of land-use intensification in Gorantalo Province, Sulawesi, Indonesia. Our focal landscape is a mosaic of forest fragments, smallholder agriculture (dominated by maize, *Zea mays* L.) and abandoned agricultural areas where woody vegetation is regenerating. We explored decomposition of different types of plant matter (leaf litter and cellulose), compared decomposition rates across habitat types, and manipulated the composition of the decomposer community (with fungi excluded or included). We also measured the abundance and community composition of the litter invertebrate community associated with our measures of decomposition. We predicted that rates of decomposition would be higher in less-modified habitats, and that the biotic and abiotic factors influencing decomposition would differ among substrates, with both fungi and litter invertebrates playing a role.

Materials and Methods

Site description

The research was conducted from 15th February – 27th April 2019 in Panua Nature Reserve (PNR), which is situated in the Pohuwato Regency (0° 31 59 N, 121° 49 30 E), Gorontalo Province, Sulawesi, Indonesia, and protected under Indonesian environmental legislation because of its biotic uniqueness. However, human disturbance, especially forest clearance for agriculture, is significant and ongoing within the reserve (Nursafingi & Holle, in review). Since 1980, forest cover in Panua Nature Reserve has been reduced by 6582 hectares, equivalent to 13.4% of the total reserve area, with an estimated annual deforestation rate of 162

hectares per year. The main deforestation driver is conversion to agriculture, which reduced the forested area by 5704 hectares (Nursafingi & Holle, in review). Panua Nature Reserve has an annual rainfall of 1500-2000 mm, with five or six consecutive wet months and three or fewer consecutive dry months (Whitten et al., 1987); the period of fieldwork corresponded to the rainy season. The study was conducted in the major habitats within the nature reserve: forests, shrublands and maize fields. We focused on human-modified forest areas within 100 m of the forest edge, subjected to varying levels of ongoing small-scale tree-cutting and adjacent to farmland. Forests of this type, rather than less-disturbed areas deeper into the protected area, are typical of the agriculture/forest matrix in human-modified landscapes of SE Asia. Forest sites had experienced low-intensity selective logging of large and emergent trees, but retained closed-canopy structure. Shrubland sites were dominated by an invasive plant species, *Chromolaena odorata* (L.) R.M. King & H. Rob. growing to 2 m tall, which produces allelochemical compounds that inhibit other plants (Laxman et al., 2019). These shrublands are formed due to abandonment after forest clearing, or when cropped maize fields are left fallow after the planting season. Maizefield sites are managed by smallholder farmers who have illegally cleared land for agriculture within the nature reserve. Sampling in the maizefields sites was started three weeks after planting, when maize stalks started to create locally shaded microclimates, allowing the study to be completed before maize was harvested approximately three months after planting. Shrubland and maize farming are both non-permanent land uses: outside of the planting season (mostly the wet season), fallow maize farmland can develop into either shrubland, bare ground, or grassland, while some shrublands are periodically cleared to plant maize.

Study design

Decomposition experiments used two different substrates, leaf litter and cellulose, representing natural sources of organic matter on the forest floor. We measured litter decomposition, cellulose decomposition and the litter invertebrate community concurrently in different habitat types at two-week intervals.

We established a study design of seven spatial blocks, with each habitat type (forest, shrubland or maize farmland) represented once within each block. Individual blocks were widely separated from each other (by distances of 0.7-18 km), ensuring appropriate replication (fig 2.1.). In six of the blocks, sites representing the three habitat types occurred within close proximity (less than 0.5 km apart), while in the seventh block the maize farmland site was

located 18 km from other habitats for practical reasons. Each habitat replicate comprised a 20x20 m plot.

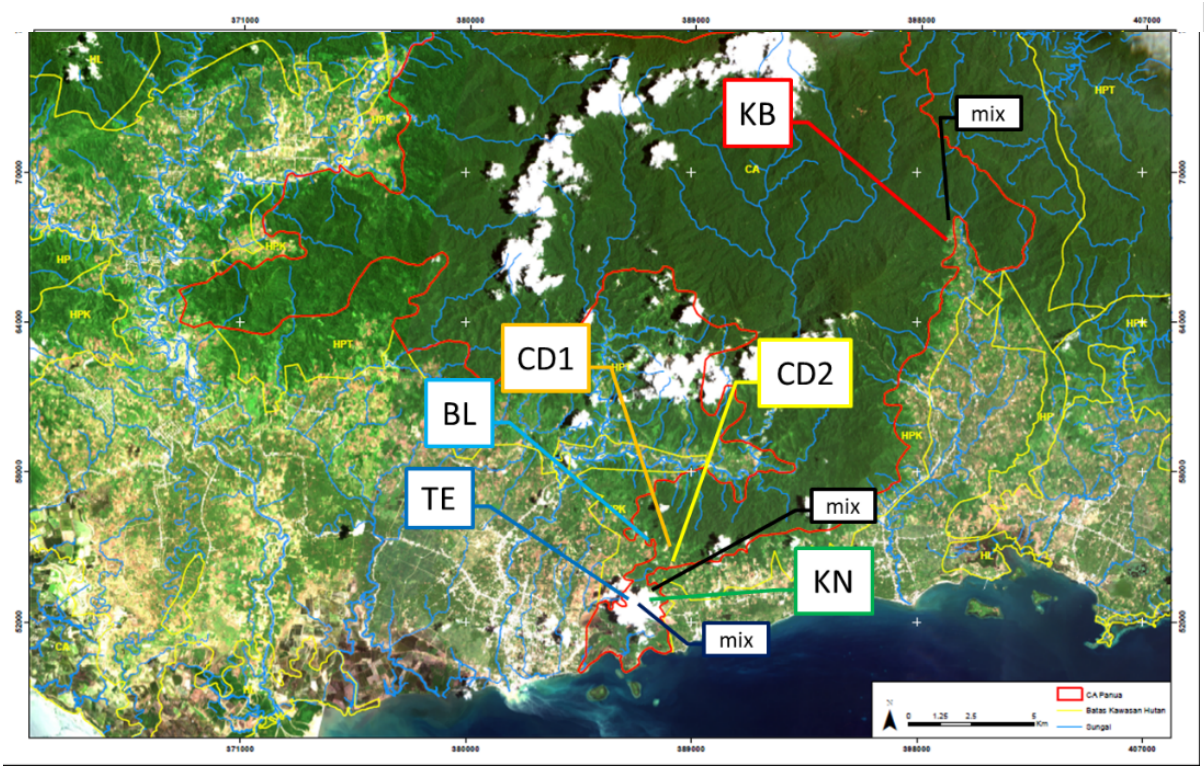


Figure 2.1. Map showing the blocked distribution of study sites within the human-modified tropical landscape of Panua Nature Reserve (reserve boundary shown in red). Block labels in the different box line colour refer to location names (KB: Karya Baru; BL: Bulangita; CD1: Cek Dam 1; CD2: Cek Dam 2; TE: Teratai; KN: Kebun Nurdin). 'Mix' is a mixed block where sites in different habitats are separated more widely (Image source: Burung Indonesia Gorontalo). Study site coordinate is available on the Appendix table a.1.

Leaf litter decomposition and litter invertebrate extraction

In each block, 108 litter bags were deployed, making a total of 756 litter bags: 7 blocks x 3 habitats (forest, shrubland, maize) x 2 treatments (fungicide, control) x 3 exposure times (2, 4, 6 weeks) x 6 replicates. Litter decomposition rates were calculated adapting methods from Powers et al. (2009). Litter was derived from fresh whole-leaves of *Macaranga* sp. trees following previous studies (Plowman & Ewers, 2012; Chellaiah & Yule, 2018); these pioneer trees are frequent but not dominant at all our study sites, making it unlikely that there will be a home-field advantage, and their leaves decompose quickly (within a month: Chellaiah & Yule, 2018). Although naturally-abscised, senescent leaves might more accurately reflect the chemistry of natural substrates, we used dried fresh leaves for our experiment, consistent with previous decomposition experiments (Moore & Fairweather, 2006; McLaren & Turkington,

2010) and because it was not feasible to collect sufficient freshly-abscised leaves. Collected leaves were exposed in full sun for three days until completely dry, indicated by their crisp texture. Larger dried leaves were broken up by hand into approximately 6 x 6 cm fragments that could be inserted into the litter bags. Each 10 x 15 cm non-degradable litter bag was filled with a 5-g sample of litter and sealed using rust-proof clips. Litter bags with coarse mesh (0.5 cm in diameter) were used to allow access to micro-, meso- and macro-fauna (Bradford et al., 2002).

In the fungus suppression treatment, litter bags containing litter were dipped in liquid fungicide (0.25 ml/L of SCORPIO 250 EC Fungicide, active ingredient difenoconazole) immediately before being placed on the ground. Controls were untreated. Sets of six litter bags were tied to a 1-meter length of cord to facilitate relocation. The distance between sets was 13 meters (Powers et al., 2009). Thirty-six litter bags per block (252 litter bags in total) were collected (two litter bags in every set every two weeks) for extraction of litter-dwelling invertebrates to assess decomposition rate changes through time in parallel with litter mass measurement. Particular care was taken when retrieving bags to minimise loss of smaller fragments through the mesh. Inevitably, some litter will be lost from coarse-meshed bags without being decomposed, but any such effect will have been consistent across treatments.

Immediately after litter bag retrieval from the field, litter was carefully removed from the bag and immediately placed in an open-topped plastic bag to ensure that no invertebrates escaped, and to avoid overheating. Samples were then transferred to Tullgren funnels as soon as possible to extract invertebrates while drying the leaf litter. The contents of each collected litter bag were exposed separately under a 15 Watt light bulb for approximately 12 hours. Extracted invertebrates were preserved in 70% ethanol. Under a digital microscope, each individual invertebrate with body size > 2 mm was counted, identified to higher taxon level, and categorised in terms of its ecological role (decomposer, omnivore, and predator) on the basis of feeding guilds. Within feeding guilds, invertebrate samples were assigned to taxon groups, mostly to Order level, but in some cases to Family (Formicidae) or Class (Chilopoda, Diplopoda). This approach of assigning taxon groups to feeding guilds is likely to be imperfect because litter fauna from the same taxon do not always occupy the same feeding guild (Ashford et al., 2013), but further identification and documentation of feeding guilds was not practicable in this species-rich and poorly-studied community within the scope of the current project. Instead, taxa which can include species within multiple feeding guilds, such as ants, were categorized into the generalist feeding guild of omnivores. Dry litter mass was measured using

a digital balance after soil particles, clinging roots, and other debris were removed by hand sorting.

Cellulose decomposition experiment

As a standardised material that represents wood, cellulose baits (single ply, unscented coreless toilet rolls) were deployed to measure cellulose degradation in various habitats for two months from 15th February – 27th April 2019. Toilet rolls have been used previously to assess termite-mediated decomposition (e.g. Leitner et al., 2018). These cellulose baits were located at the same sites as the litter bag experiment. In total 126 toilet rolls (7 blocks x 3 habitats x 6 replicates per block) were used. The toilet rolls were not dried initially. They had very low water content, were used directly after removal from plastic packaging, and varied little in initial mass. Recollected toilet rolls were dried in direct sun for three days until completely dry, indicated by their constant dry mass. Cellulose decomposition was calculated by subtracting remaining toilet roll mass from the initial toilet roll mass (33.89 g ± 0.20 (SD)).

Data analysis

Decomposition data were expressed as decomposed litter mass and as a decomposition rate (k), following Guendehou et al. (2014), to evaluate the decomposition process and to measure the speed at which leaf litter is broken down by decomposers respectively. Decomposition rate (k) was estimated using a negative exponential equation:

$$X_t / X_0 = e^{-kt} \qquad \text{eqn 1 (Olson, 1963)}$$

where X_t is litter mass at time t, and X_0 is original litter mass, and X_t / X_0 is therefore the fraction of the original litter mass remaining at time t. Where litter was completely decomposed, litter mass values of zero were input as 0.01g to allow k value calculations. After calculating k values for the seven replicate sites of each habitat, we used linear mixed-effects models to assess the effects of habitat type on decay rates, with block as a random effect. The k values were log-transformed for these analyses as heteroscedasticity was detected in the standardised residuals.

All statistical analyses and graph plotting were performed using R (R Core Team, 2021). Analyses used data from all blocks with the exception of analyses of litter invertebrates, for which data were missing for the KB block. The effects of time of incubation, habitat type and invertebrate community on decomposed litter mass were analysed using linear mixed effects models (using the *lme* function in the *lme4* or *nlme* package) with habitat type, fungicide treatment and litter invertebrate abundance as fixed factors and block as a random effect. Full models with interactions were fitted, and then non-significant interaction terms dropped from

the model until the minimal adequate model was obtained according to the AIC scores. The minimal adequate model was the best model as judged by AIC, so the effects of explanatory variables on decomposed litter mass were reported using this model. Analysis of variance (ANOVA) was conducted to compare means among groups. To identify the groups that differed significantly, linear mixed-effects model analysis was followed by post-hoc analysis with Tukey Contrasts test using the *glht* function in the *multcomp* package in R.

To compare decomposition of leaf litter and cellulose we analysed the effects of habitat type on decomposition using data from week 6. Linear mixed effects models (using the *lme* function in the *lme4* or *nlme* package) were used to test the effects of habitat type and fungicide as fixed factors and block as a random effect (Bates et al., 2015). Analysis of Similarity (ANOSIM) (*anosim* function in the *vegan* package) was used to test for statistical differences among the invertebrate communities of the three habitat categories and two fungicide treatment categories (Dixon, 2003; Oksanen, 2022). Analyses focused on invertebrate relative abundance data obtained from the litterbags extracted at week 2 of the experiment, to avoid underestimating abundances; rapid decomposition meant that leaf litter mass was much reduced in later weeks, likely limiting invertebrate colonisation and occupancy. Sampling points where no invertebrates were recorded were omitted from the analysis.–Data were visualised using a Non-metric Multi-dimensional Scaling (NMDS) plot, generated in *ggplot* using the Bray-Curtis distance measure.

Results

Effects of habitat, fungicide, and time on litter decomposition

Remaining litter mass decreased significantly with time ($F_{1, 698}$=364.03, p <0.001), and differed significantly among habitats ($F_{2, 698}$=130.76, p <0.001). Remaining litter mass was lowest in forest, highest in maize, and intermediate in shrubland, with all pairwise comparisons statistically significant (Tukey Contrasts test). There was no significant effect of fungicide on litter decomposition ($F_{1, 698}$=6.71, p=0.43) (Table 3). Although the interaction between fungicide treatment and time was significant ($F_{1, 671}$=4.49, p <0.03, linear mixed effects model), the best-fitting model on the basis of comparing AIC values did not include the interaction term.

Similarly, decomposition rates measured using *k* values differed significantly across habitat types ($F_{2,11}$=12.823, p=0.0013). Rates were highest in forest (0.293±0.03 (SE)), lowest in maize (0.127±0.01 (SE)), and intermediate in shrubland (0.224±0.02 (SE)), with all pairwise

comparisons statistically significant (Tukey Contrasts test) except the comparison between forest and shrubland (fig. 2.3.).

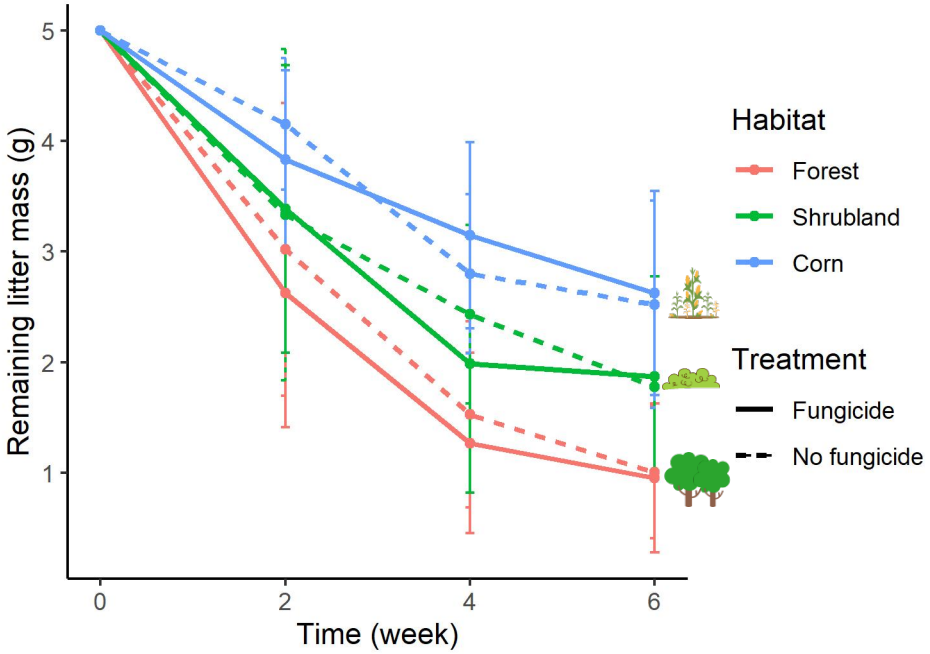


Figure 2.2. Remaining mass of *Macaranga* sp. leaf litter in three habitats measured every two weeks (n=689). Error bars show standard errors of the mean.

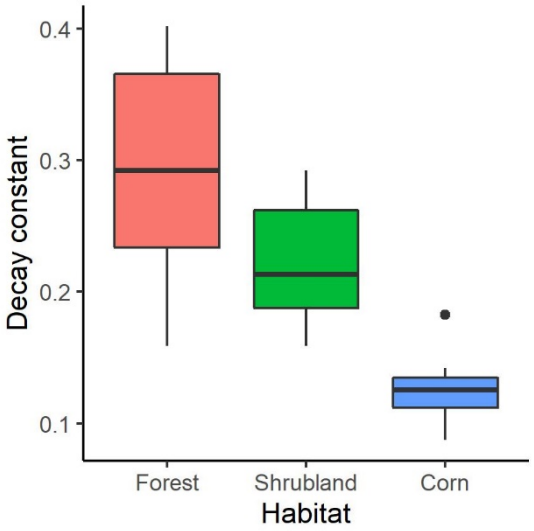


Figure 2.3. Decay constant (k) of *Macaranga* sp. leaf litter in three habitats (n=20 sites spread across 7 blocks; data missing for one Shrubland site). The boxplots show the median (central bar), upper and lower quartiles, and whiskers including points within 1.5 interquartile range. Dots outside of the boxplots are outliers.

Analysing litter decomposition in the final retrieval at week 6 (fig. 2.4.), the mass of litter remaining differed significantly among all habitats (Tukey contrasts test). Decomposition was highest in forest, lowest in maize plantations, with shrubland intermediate ($F_{2, 212}$=78.62,

p <0.001). There was no significant effect of fungicide ($F_{1,212}$=0.71, p =0.39). Cellulose degradation differed significantly among habitats ($F_{2,89}$=25.54, p <0.001), with mass remaining significantly lower in forest than shrublands and maize, which did not differ significantly from each other (Tukey Contrasts test).

Comparison of decomposition of leaf litter and cellulose across habitat types

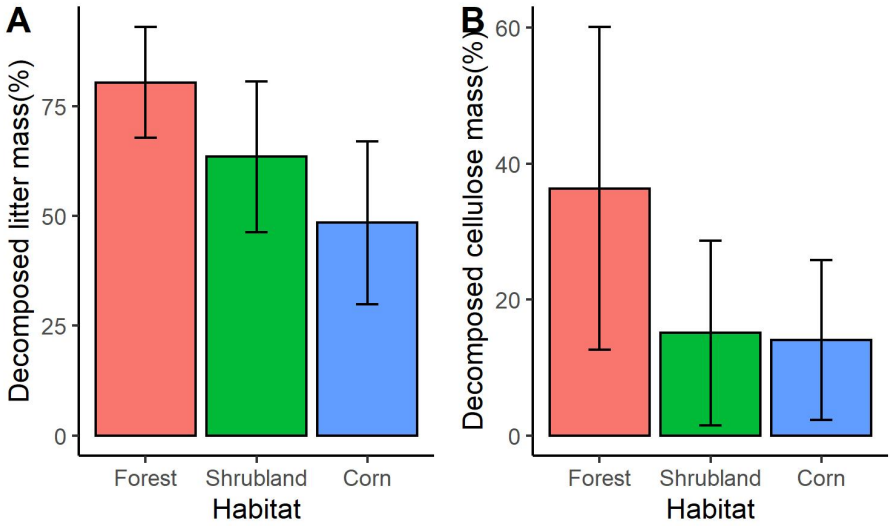


Figure 2.4. Decomposed mass of (A) leaf litter (n=222) and (B) cellulose (n=98) exposed in three habitat types and retrieved after six weeks. Visualisation in (A) disregards the fungicide treatment which had no significant effect on decomposition. Error bars show standard errors of the mean.

Litter invertebrate abundance in different habitats and through time for different feeding guilds

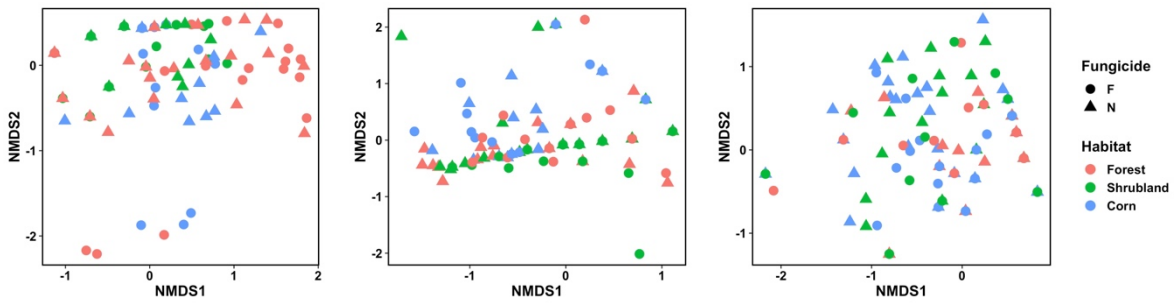


Figure 2.5. Non-metric multidimensional scaling (NMDS) of litter invertebrate community composition in relation to habitat types and fungicide treatments for three separate periods of litterbag exposure, which are in 2 (left), 4 (middle), and 6 (right) weeks. Each habitat type is represented by a different colour and the fungicide treatment is indicated by symbol shapes. The Bray-Curtis dissimilarity index was used for determination of dissimilarities among litter invertebrate communities. Stress value are 0.1148, 0.100, and 0.119 for week 2, 4 and 6 respectively indicating good fit of the models.

We identified 3572 individual litter invertebrates in total. Total abundance was highest in forest sites (1571 individuals) followed by maize farming (1093 individuals) and shrubland

(906 individuals). Total abundances of decomposers, omnivores, and predators were 694 (19.42%), 2763 (77.35%), and 115 (3.22%) individuals, respectively, which differed significantly. Based on the week 2 relative abundance data, there was a statistically significant difference in litter invertebrate community abundance between habitats (ANOSIM, R=0.028; p=0.0356). No significant fungicide effects on invertebrate abundance were detected in any week (ANOSIM, p>0.1).

Discussion

Our study documents the effects of habitat modification on multiple dimensions of decomposition in a tropical setting, alongside changes to the litter invertebrate community. We found that habitat modification altered decomposition consistently for both leaf litter and cellulose substrates, with reduced rates in more modified environments.

Effects of habitat modification on decomposition of plant substrates

Litter decomposition was most rapid in the forest sites, lower in shrubland, and lowest in maize farmland. This is consistent with previous studies that have found lower decomposition rates in agricultural sites compared with natural or less-modified sites in tropical regions (Didham, 1998; Attignon et al., 2004; Kagezi et al., 2016), especially at low elevations (Becker & Kuzyakov, 2018). Land-use change from tropical forest to intensively managed agricultural land has been shown to affect functional trait composition; this could impair the functional stability of litter invertebrate communities, with managed monoculture plantation tending to have more inconsistently assembled and compositionally unstable communities (Mumme et al., 2015).

Higher decomposition rates are to be expected in closed canopy-sites, where litterfall input will be high (Paudel et al., 2015), supporting high decomposer biomass and activity. Microclimatic conditions in these habitats are also expected to favour decomposer activity (Lodge et al., 2014). Like leaf litter decomposition, cellulose decomposition was higher in the forest habitat. Our maize farming and shrubland sites experience negligible natural inputs of woody material, so low prevalence of cellulose-adapted taxa in these habitats is likely to have limited the capacity of decomposer communities to process cellulose baits. Wood and cellulose decomposition in tropical rainforests is often mediated by termite activity (Jouquet et al., 2011; Leitner et al., 2018; Ashton et al., 2019). However, termites were not the sole decomposers of cellulose baits in our experiment, with large-bodied millipedes, specifically *Salpidobolus* sp., also having an important role (JH, personal observation). The main correlates and drivers of wood decomposition rates remain uncertain. For example, while some studies show that wood

decomposition is more influenced by temperature than by tree species and decomposer diversity (e.g. Pietsch et al., 2019) others have concluded differently (e.g. Dossa et al., 2016).

The absence of fungicide effects on leaf litter decomposition

Surprisingly, fungicide treatment did not slow leaf litter decomposition or lower decomposition rates in any of the three habitats. At face value, this suggests that the contribution of fungi to decomposition in our system is small compared to that by litter invertebrates. There are four alternative explanations for this result. First, our methods may have been ineffective in suppressing fungal activity, perhaps because we used low fungicide concentrations corresponding to the minimum recommendations of the manufacturer, or because the active ingredient in our fungicide, difenoconazole, had low effectiveness (Masiello et al., 2019). A previous study found that the azole fungicide tebuconazole had no significant effect on leaf consumption by the aquatic amphipod crustacean *Gammarus fossarum* unless at very high concentrations (500 µg/L) (Elskus et al., 2016). Second, fungus-mediated decomposition is improved by nutrient enrichment (Pascoal & Cassio, 2004), and fungal decomposition activity is decreased as a result of the low-nutrient content in tropical soils (Yeong et al., 2016). A third possible mechanism is that, as the study took place during the rainy season, the fungicide treatment may have been ineffective because of rapid leaching during rainfall events (Lorenz et al., 2017). Finally, the role of fungi in decomposing leaf litter could be taken over by other taxa, such as invertebrates. Macrofaunal contributions to leaf litter decomposition can range widely, from 1.6% to 66% depending on litter type and climatic conditions (Slade & Riutta, 2012). The *Macaranga* sp. leaves we used do not contain high amounts of heavier structural compounds such as lignin, cellulose and fibre which are associated with high leaf tensile strength (Chellaiah & Yule, 2018). Thus, *Macaranga* leaves may be relatively susceptible to invertebrate feeding and mechanical fragmentation.

We grouped litter invertebrates into three feeding guilds: decomposers, omnivores, and predators. Categorizing invertebrates by their functional group can be a robust approach for assessing ecosystem conditions (Cummins et al., 2005; Menezes et al., 2010) and evaluating impacts of land use change (Schulze et al., 2004). Invertebrate abundance responded idiosyncratically among different habitat types. Litter invertebrate relative abundance was different among habitat types and was reduced in human-modified maize and shrubland. This is consistent with previous studies documenting that land use change from forests to agriculture altered invertebrate communities in both tropical (Barnes et al., 2014; Edwards et al., 2012; Jones et al., 2003) and temperate ecosystems (Eggleton et al., 2005). Resource availability

might drive this pattern, with forest habitat providing greater and higher-quality food for litter invertebrates (Richardson et al., 2005). The more leaf litter, the more litter invertebrates are available to colonise litter bags. Alongside reduced litter abundance, reduced litter diversity could also contribute to these patterns. Litter diversity is correlated with vegetation diversity, which inevitably declines when diverse tropical forests are modified or converted to agricultural monocultures (Gillison et al., 2003). Nonetheless, existing data suggest that litter quantity has a greater effect on litter invertebrates than litter diversity (Lu et al., 2016).

Consistent with the result for decomposition, fungicide treatment did not affect the litter invertebrate community significantly in our experiment. While some studies have demonstrated that fungicides negatively affect invertebrate communities (Fernández et al., 2015; Flores et al., 2014), others report contrasting results, suggesting that fungicide toxicity is variable or context dependent. Fungicide concentrations may not have exceeded the tolerance range of litter invertebrates in our study, and higher concentrations might be expected to have more pronounced impacts, as documented in previous studies (French & Buckley, 2008; Zubrod et al., 2017). Furthermore, long-term and repeated exposure to low fungicide concentrations could increase chronic effects (Elskus et al., 2016).

Conclusion

Habitat modification markedly reduced decomposition rates of both litter and cellulose. Across all habitat types our data are consistent with a minor role for fungi in decomposition of these substrates, relative to litter fauna. Studies quantifying the contribution of litter decomposition to nutrient inputs in the soil, and further investigating how decomposer biodiversity affects decomposition will be needed to better understand the effects on land-use change on ecosystem services mediated by decomposers, as well as the biotic and abiotic mechanisms involved.

Chapter 3: Proximity to rainforest increases predation of model caterpillars in tropical maize fields

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Author contribution

MJMH carried out the fieldwork, analysed the data, and wrote the manuscript. OTL provided suggestions and ideas on experimental design and commented on the manuscripts.

Abstract

In many tropical countries, the rural landscape comprises a mosaic of agricultural areas and forest remnants. Forests adjacent to agricultural areas can export ecosystem services such as predator-mediated biological pest control. We used model plasticine caterpillars to assess predation of insect herbivores (potential pests) in a human-modified landscape in Sulawesi, Indonesia, comparing three habitat types (forest, shrubland, and maize fields), and along transects running from the forest into maize fields. Attack frequency on plasticine caterpillars was significantly lower (by up to 18.6%) in maize fields compared to other habitats and was caused mostly by arthropods. Predator attacks in maize were substantially (34.7%) higher at sampling points close to the forest edge. Our data suggest that habitat conversion erodes the ecosystem service of predation, and that predation of insect pests within the crop is likely to be forest-dependent, providing a possible incentive for forest conservation measures in human-modified tropical landscapes. It remains to be established whether spillover of predators and associated pest predation services limit pest populations and associated crop damage, especially during outbreak periods.

Keywords: Tropical forest, Sulawesi, predation, herbivorous insect, spillover, small-scale agriculture.

Introduction

Tropical forests are under severe threat, mainly from agricultural expansion and intensification (Gibbs et al., 2010; Carrasco et al., 2017), with almost 6 million hectares of tropical forests now converted for agricultural purposes (Mayaux et al., 2005). Conversion of forests to agriculture is driving a biodiversity crisis in Southeast Asia (Sodhi et al., 2010; Wilcove et al., 2013), which has the highest annual rate of deforestation and forest degradation among tropical regions (Mayaux et al., 2005; Miettinen et al., 2011; Stibig et al., 2014).

Agricultural production relies on ecosystem services that tropical forest ecosystems provide, including pollination (Blanche et al., 2006) and pest control services (Gray & Lewis,

2014; Lemoine et al., 2017). Pest control services involve biological control by natural enemies such as predators and parasitoids (Tscharntke et al., 2005; Power, 2010). Insect pests are a predominant cause of yield losses in many of the most important tropical crops (Oliveira et al., 2014). As an alternative to high-input and often environmentally harmful pesticides, these pests can often be limited naturally by top-down control (Zhang & Adams, 2011). In tropical agriculture, predation of insect herbivores is dominated by arthropods and mammals (Denan et al., 2020). Predation rates peak at low latitudes and elevations (Roslin et al., 2017), and in sites where plant diversity is high (Leles et al., 2017). Hence, insect predation is expected to reach its highest rate globally in lowland tropical habitats.

Most studies of predation services in tropical Southeast Asia have focused on perennial crops such as oil palm, rubber, orchard fruits, and cotton (Howe et al., 2009; Nurdiansyah et al., 2016; Denan et al., 2020). Maintaining ground layer vegetation in perennial crops such as oil palm can create habitat for pest enemies (Ashton-Butt et al., 2018), making the crop less susceptible to pest attacks (Luke et al., 2019). Seasonal and annual crops such as rice, wheat, maize, soybeans, and tobacco are more affected by the insect pests than perennial ones (Oliveira et al., 2014), but have received much less attention in this context. Studies on predation in a forest-maize landscape mosaic has been conducted in Latin America (Ferrante et al., 2017) and Africa (Jordon et al., 2021), but we are unaware of equivalent studies in the tropical landscape of Southeast Asia.

Of particular interest is the extent to which pest control services are forest dependent. While some studies have found limited evidence for 'spillover' of predators from forest fragments to agroecosystems (Gray & Lewis, 2014), others have shown that at least some insect taxa have elevated species richness or abundance in agricultural land adjacent to forests (Lucey & Hill, 2012; Lucey et al., 2014). Spillover effects of predation can occur bidirectionally, from natural habitats to managed land and *vice versa* (Blitzer et al., 2012). Where spillover occurs, it can nonetheless be ineffective in reducing pests (Tscharntke et al., 2016). Such effects can also vary temporally; for example predator spillover from natural habitats into nearby farmland can occur during the early stages of crop growth, but be reversed later in the season (Rand et al., 2006).

Here we investigate predation of mimic insects across a habitat-modification gradient within a forest-farmland landscape in Sulawesi, Indonesia, comparing three habitat types: forest fragments, smallholder agriculture (dominated by maize) and fallow fields dominated by an invasive shrub. In addition, we investigated predator attack rates within the crop at different distances from the forest edge. To quantify predation risk we use plasticine caterpillars (models

made using modelling clay such as plasticine) which have been used widely to assess predation of insect herbivores in a range of natural ecosystems, and to quantify pest control services in agroecosystems (Howe et al., 2009; Gray & Lewis, 2014; Ferrante et al., 2017; Lövei & Ferrante, 2017; Denan et al., 2020). We hypothesised that habitat modification would reduce predation of insect herbivores, and that (within the maize crop), predation rates would decline with distance from nearby forest fragments.

Materials and methods

Study site

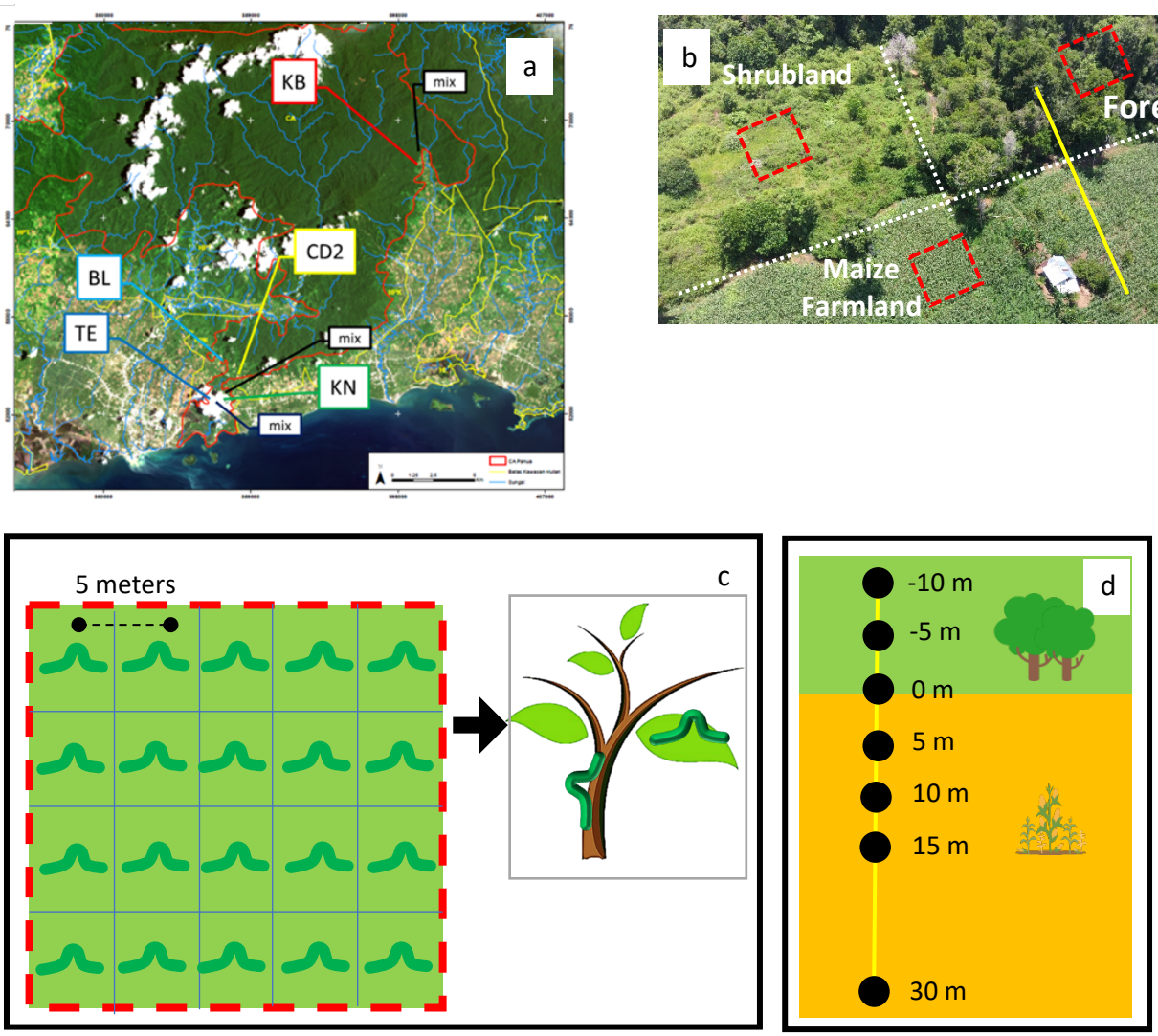


Figure 3.1. Study sites in Panua Nature Reserve. (a) Block distribution within Panua Nature Reserve (Image source: BPKH XV Gorontalo). (b) Schematic sampling design for assessing ecosystem functioning in the different land-uses within each block (red dashed boxes) and a transect with sampling at different distances from the forest interior into the crop (yellow line). (c) Plasticine caterpillar positions in each of the six replicate sites of each habitat. (d) Layout of a single transect showing positioning of plasticine caterpillars at various distances from the forest edge into to the maize farmland.

Data were collected between 15th February – 27th April 2019 in Panua Nature Reserve (PNR), situated in the Pohuwato Regency (0° 31 59 N, 121° 49 30 E), Gorontalo Province, Sulawesi, Indonesia. While PNR is a protected area, it experiences significant forest clearance. Since 1980, forest cover in Panua Nature Reserve has been reduced by 6582 hectares, equivalent to 13.4% of the total reserve area, with an estimated deforestation rate of 162 hectares per year. The main deforestation driver is agriculture, which caused 5704 hectares of forest loss (Nursafingi & Holle, in review). PNR has an annual rainfall of 1500-2000 mm, with five or six consecutive wet months and three or fewer consecutive dry months (Whitten, Mustafa, & Henderson, 2002). The period of fieldwork corresponded to the rainy season. We collected two complementary data sets on predation of caterpillars (1) across habitat types, and (2) along transects from the forest into the crop.

Plasticine caterpillars

Plasticine caterpillars were used as a proxy for predation rates of predators such as arthropods, birds, reptiles, and mammals that allows a direct quantification of predation risk in the field setting (Lövei & Ferrante, 2017). Previous work using similar methods has included investigations of how predation varies in relation to forest fragmentation (Koh & Menge, 2006; Leles et al., 2017), at different latitudes and elevations globally (Roslin et al., 2017), and in different tropical crops (Denan et al., 2020). Non-toxic plasticine modelling clay (Newplast light green) plasticine caterpillars were formed by rolling modelling clay on a smooth surface and cutting it into cylinders 3 mm wide and 15 mm long. Consistent with previous studies, plasticine caterpillars were shaped to copy the 'inchworm' larvae of moths in the family Geometridae, which are abundant herbivores in many natural and agricultural systems (Leles et al., 2017). This method might more appropriately be interpreted as providing a measure of predation risk rather than absolute predation rates, because plasticine caterpillars lack important thermal, visual, olfactory, and movement cues that are used by predators (Murray et al., 2020). For example, parasitoid wasps that rely on chemical cues are unlikely to attack plasticine caterpillars (Ferrante et al., 2021).

Across-habitat study

We investigated the three major habitats within the nature reserve: forests, shrublands and maize fields. Forest sites included in our study all had intact canopy cover but had experienced small-scale timber extraction. Primary forest in PNR is more remote from human settlements and cultivated areas and were not included in our study as they are less relevant in the context of pest predator spillover. Shrubland and maize farming are non-permanent land-

uses. Shrublands represent areas previously cleared of forest and which may have been cultivated previously and then abandoned or left fallow. Shrubland sites were dominated by the invasive plant *Chromolaena odorata*, which produces allelochemical compounds that inhibit growth and germination of other plants (Laxman et al., 2019). Maize is planted mostly during the wet season (January to April) and this land may be uncultivated (mostly bare soil or herbaceous weed or grass cover) during drier periods. We conducted the study during the critical vegetative phase of maize growth, when pest attacks on foliage and leaf sheaths, including by larvae of the important pest species fall armyworm (*Spodoptera frugiperda* (J.ESmith)), can lead to reduced fruiting and kernel production (FAO, 2018; Kumela et al., 2018). In our study area we observed that, in extreme cases, caterpillars could consume the foliage of entire maize plants, killing them at an early vegetative stage.

We established a blocked design with six blocks. In five of the blocks, each of the three habitat types (forest, shrubland or maize farmland) was represented in close proximity. Individual blocks were widely separated from each other (by distances of 0.7-18 km) ensuring appropriate replication (fig. 3.1.a-b). In the sixth block (labelled 'mix' in fig. 3.1.), the three habitats were more widely separated for practical reasons. Analysis of predation data without this additional block did not change the overall result qualitatively. At each site, two plasticine caterpillars (one glued to a leaf and one glued to a stem) were deployed at each of twenty-five points (located on a 5m x 5m grid (fig. 3.1.c), totalling 900 caterpillars across all blocks. Caterpillars were attached to the upper leaf surface, approximately 1.5 m above the ground (Bruno et al., 2017) when maize plants were four weeks old using UHU® adhesive super glue as it remains a common method used to attach plasticine caterpillars to plants (Czarnecki et al., 2022; Ferrante et al., 2021; Tvardikova & Novotny, 2012), but caterpillars secured in this way may be more likely to be dislodged than those attached using entomological pins (as used in some previous studies; (Tvardikova & Novotny, 2012).

Plasticine caterpillars were left in position for 3 days (or 4 days for BL, CD2, and KN blocks when the weather conditions did not permit safe recollection after 3 days), with the duration of exposure always consistent within a block. The ground was searched to check for caterpillars that might have fallen from the vegetation. These represented <5% of all caterpillars. Data for fallen caterpillars were analysed alongside data for those that remained *in situ*. There is uncertainty as to whether attacked plasticine caterpillars recovered from the ground were attacked in their initial position or after they had fallen, and attack rates may be higher at ground level (Ferrante et al., 2019). However, the number of plasticine caterpillars affected in this way was small (<5% of all caterpillars), making it unlikely that overall trends

were affected. About 30% of all caterpillars were not recovered in this experiment. We could not identify whether these were completely removed by predators, attacked and dropped but undiscoverable, or remained un-attacked but lost. However, the incidence of missing caterpillars was consistent across habitats, with 95 (31.67%), 92 (30.67%), and 74 (24.67%) lost in forest, shrubland, and maize farmland habitats, respectively, making it unlikely that these missing data will bias overall results.

Transect study

To investigate whether forest fragments contribute functionally to pest control in nearby farmland, this component of the study focused on the forest / maize farmland interface. Seven linear transects (KN1, KN2, KN3, KN 4, PT1, PT2, PT3) were established running from 10 m within the forest and up to 30 m into the maize farmland. Three replicates of ten caterpillars were deployed at each of 7 positions: -10 m, -5 m, 0 m, 5 m, 10 m, 15 m, and 30 m relative to the forest edge (10 caterpillars x 3 replicates x 7 distances x 7 transects, fig. 3.1.d). All caterpillars were adhered to the maize plants, which were around 50 cm apart. Because plasticine caterpillars were not set up in the 30 m distance at the PT3 transect, the total of the plasticine caterpillars used in this study was 1440. We did not collect data at locations deeper into the forest because our focus was on transfer of pest control services from forest to farmland.

Each plasticine caterpillar was attached using UHU® strong glue to the upper surface of a leaf of a different plant individual (maize plants, or a range of saplings and shrubs within the forest) approximately 1.5 m above the ground. Plasticine caterpillars were left in position for two days and then recovered to score for predator damage. Where caterpillars were missing the ground was searched to check for caterpillars that had fallen from the vegetation.

Plasticine caterpillar retrieval and bite mark identification.

After collection, caterpillars were scored according to presence of bite marks and the type of marks. Where there was uncertainty about the identity of the predator the bite marks were photographed for later close inspection. Bite marks were attributed to broad predator categories (arthropods, birds, mammals, reptiles) according to identification guidelines for the Asia-Pacific region (Low et al., 2014).

Data analysis

Statistical analyses and graphical visualization were performed using R (R Core Team, 2020). We excluded missing plasticine caterpillars from analyses. For the across-habitat study,

we calculated the total number of plasticine caterpillars attacked or not at each site (n = 18 sites across 3 habitat types, 6 blocks), for all potential predators and two positions (leaf and stem) combined. To investigate predation by the dominant predator group, arthropods, across habitats and on leaves and stems, we fitted models with habitat type and position on leaves versus stems as explanatory variables, with and without an interaction term. Full models with interactions were fitted, and then non-significant interaction terms dropped from the model until the minimal adequate model was obtained according to the AIC score. We used combined attacked and non-attacked plasticine caterpillars as a two-column response variable in Generalized Linear Mixed-Effects Models (GLMM) (fitted by maximum likelihood), using the *glmer* function in the *lme4* package, specifying a binomial error structure and block as a random effect. Analysis of variance (ANOVA) using the *anova* function was conducted to compare means, followed by post-hoc analysis with Tukey Contrasts tests using the *glht* function in the *multcomp* package.

For the transect study, the effects of distance to the forest edge on the proportion of plasticine caterpillars attacked by arthropod predators were analysed using a mixed effects models (using the *lme* function in the *lme4* package) with distance as a continuous explanatory variable and transect as a random effect. To assess the effects of distance from the forest edge on predation of caterpillars, the analysis was restricted to data from maize farmland data points.

Results

Predation of caterpillars *across habitats*

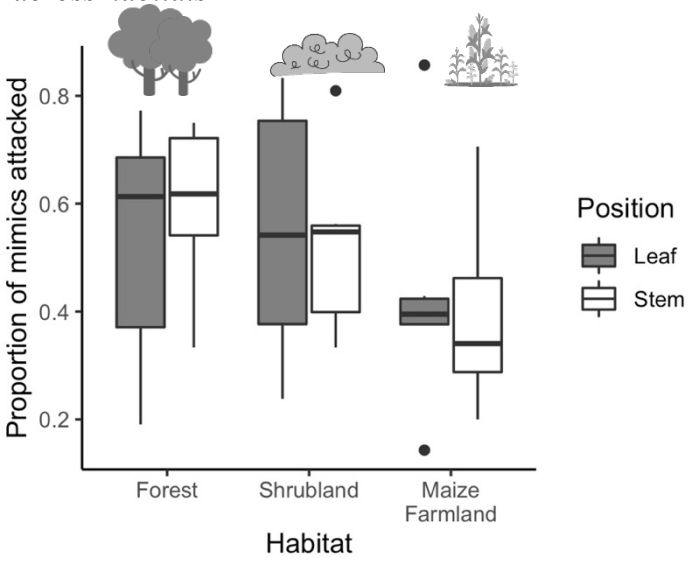


Figure 3.2. The proportion of plasticine caterpillars attacked by any predator across habitat types. Data are plotted separately for plasticine caterpillars attached to leaves and stems. The boxplots show the median

(central bar), upper and lower quartiles, and whiskers including points within 1.5 interquartile range. Dots outside of the boxplots are outliers.

We recovered 639 of the 900 plasticine caterpillars of which 316 (49.5%) were attacked (295, 10, 8, and 1 by arthropods, birds, mammals and reptiles, respectively). We did not record more than one class of enemy attacking individual caterpillars. The percentage of caterpillars predated was highest in forest habitats (57.1%), followed by shrubland (53.8%) and maize (38.5%). The most parsimonious model as judged by AIC did not include a habitat x position interaction. Post-hoc Tukey contrast tests suggest that forest and shrubland predation rates did not differ significantly ($p=0.76$) but both forest and shrubland had significantly higher predation rates than maize farmland ($p<0.001$ and $p=0.009$ respectively). As attacks on plasticine caterpillars were dominated by arthropods, separate analyses of arthropod predation showed very similar results to the full analysis. Attack rates did not differ significantly between stems and leaves ($p=0.81$; fig. 3.2.).

Predation of caterpillars *in maize farmland in relation to distance from the forest edge*

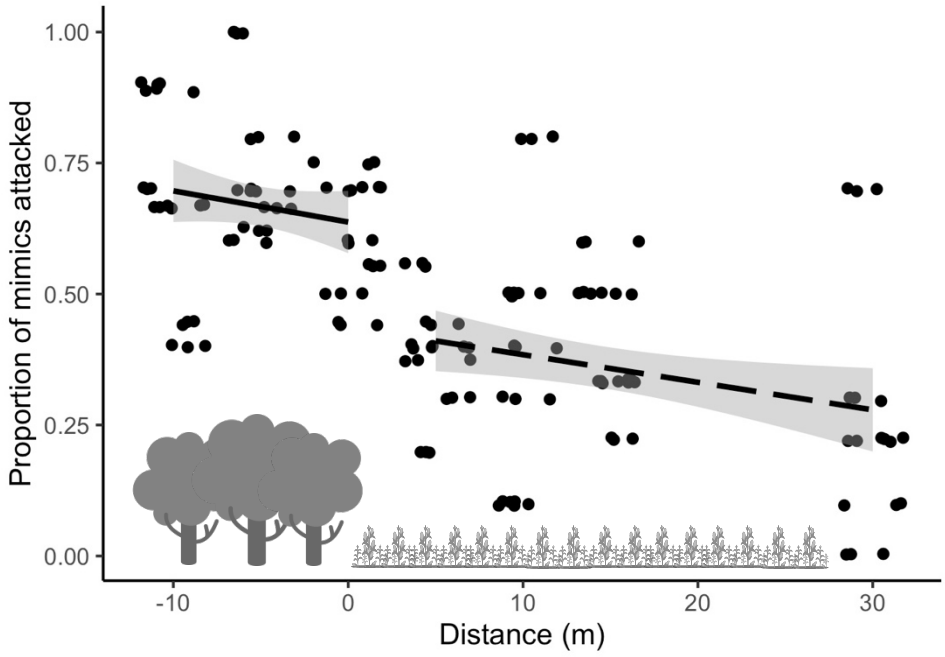


Figure 3.3. The proportion of plasticine caterpillars attacked by arthropod predators at different distances relative to the forest edge. Grey shading represents the 95% confidence interval for predictions from a linear model. Solid and dashed lines represent linear regression of datapoints in the forest and maize farmland, respectively. Plotting of data points has been jittered for clarity.

In the transect study, we recovered 1377 of 1440 caterpillars (95.62%) in total of which 681 (49.5%) were predated. The proportion of attacked caterpillars at -10 m, -5 m, 0 m, 5 m, 10 m, 15 m, and 30 m were 66.7%, 73.1%, 60.6%, 37.9%, 37.9%, 40.90%, and 25.9%

respectively. Attacks on plasticine caterpillars were significantly higher in sites closer to the forest ($F_{1,73}$=5.60, p=0.021; fig. 3.3.). In a separate analysis, there was no significant distance effect on attack rates in the subset of forest data points (-10, -5, and 0 m from the forest edge; $F_{1,55}$=2.4, p=0.127).

Discussion

Spillover of ecosystem services from forest remnants into agricultural crops is widely discussed as a possible incentive for reconciling agricultural production with conservation objectives (Grass et al., 2019). Although experiments using plasticine caterpillars to mimic insect herbivores have been used to examine predation across various habitats in the Asia-Pacific region, most such studies focus on perennial plantations and agroforestry systems (Howe et al., 2009; Nurdiansyah et al., 2016; Denan et al., 2020), and studies that focus on insect predation in landscapes with annual crop agriculture are scarce. Similar studies within maize crops have been conducted in Latin America and Europe (Ferrante et al., 2017, Ferrante et al., 2019), but we believe that ours represents the first such study in Southeast Asia.

Habitat modification reduces predation of insect herbivores

Overall, predation of plasticine caterpillars by any predator was significantly lower in maize farmland, the most modified habitat investigated, compared to forest or shrubland. This is consistent with a study in the Argentina, where predation rates in forest were also higher than in maize (Ferrante et al., 2017). Reduced predator activity in maize farmland could reflect the reduced plant diversity and habitat complexity within the crop, relative to non-crop habitats, as well as increased tillage and other disturbance. It seems likely that arthropod attacks in our study can be attributed predominantly to ants (Hymenoptera, Formicidae), as in previous studies (Perfecto, 1991; Offenberg, 2015; Denan et al., 2020; Rossi et al., 2022). Increased leaf-litter diversity and quantity in the more structurally complex and permanent vegetation of the forest and shrubland are likely to provide more favourable nesting locations for ants (Leles et al., 2017). While the shrublands studied here lack the high plant diversity of the forest habitats, predation rates were similarly high. The presence of relatively permanent ground vegetation in shrubland habitats is likely to provide habitat for ants and other arthropod pest enemies (Ashton-Butt et al., 2018).

Attacks on plasticine caterpillars by vertebrate predators like birds and mammals were much less frequent than attacks by arthropods, consistent with the overall trend for arthropod predators to dominate at lower latitudes and elevations (Roslin et al., 2017). However, low predation by vertebrates may in part reflect the sampling period, which was during the

vegetative growth phase of the maize; in Latin America, attacks on plasticine caterpillars by vertebrates peaked at cob ripening or during the flowering period (Ferrante et al., 2017). The low number of bird attacks on plasticine caterpillars in our study contrasts with results of a previous study in cacao agroforestry in Indonesia, where the endemic lemon-bellied white-eye *Zosterops chloris* was identified as the main driver of predation on artificial prey (Maas et al., 2015). Unlike agroforestry systems, tree-poor monoculture maize plantations are unlikely to be attractive foraging sites for most insectivorous birds (Lemessa et al., 2015; Srinivas & Koh, 2016).

Caterpillar arthropod predators are forest-dependent.

Predation of plasticine caterpillars was higher at sampling points close to the forest edge compared to those further into the maize crop (fig. 3.3.). This might indicate that forest fragments serve not only as a spillover source of arthropods to the nearby farmland (Lucey & Hill, 2012; Lucey et al., 2014), but also spillover arthropod-mediated insect predation. Different ecosystem functions are likely to vary in the degree to which they spillover to non-natural habitats, linked in part to the degree of mobility of the organisms mediating the different functions. For example, in the same landscape we found that invertebrate-mediated decomposition in forest habitats was higher than that in the maize farmland; however, in the case of decomposition there was no correlation between decomposition in the crop and distance from the forest edge (Holle & Lewis, 2022; Chapter 2).

A previous study in tropical Latin America (Ferrante et al., 2017) also found that predation pressure was higher in forest fragments than in nearby cultivated habitats. However, Ferrante et al., (2017) did not record a significant change in predation with proximity to forest fragments (Ferrante et al., 2017). These differences might in part reflect genuine differences in predator identity, activity and impact between the two landscapes; for example, Ferrante et al. (2017) record a much higher incidence of vertebrate attack in their study. Methodological may also contribute to the contrasting outcomes. For example, in our study we deployed plasticine caterpillars on foliage or stems in an attempt to mimic the location of pest caterpillars, while Ferrante et al., (2019) attached mimic caterpillars to a standardised substrate (a reed section) to minimise handling damage. This, and the different design of plasticine caterpillar used, could potentially alter encounter rates with ants foraging in different strata.

Conclusion

Overall, our results suggest that the activity of predators of insects such as caterpillars is significantly reduced in maize-dominated farmland, relative to nearby forest and shrubland

habitats, but that predation services from arthropods (likely to be dominated by ants) are transferred from forests to nearby farmland. The relatively high rates of predation observed in shrubland habitats hint that spill-over from these non-forested fallow habitats could also elevate predation in nearby crops but testing this would require further study. Ants can be important pest control agents in agriculture (Offenberg, 2015), and the observed pattern of attack on plasticine caterpillars suggests that landscape-level approaches to maintaining forest or shrubland set-asides with these human-modified landscapes could help sustain crop yields. However, the benefits of the observed patterns of predator attack for crop yields are untested, and it remains uncertain whether the observed levels of predation would be sufficient to provide substantial pest control services, especially during pest outbreaks (Tscharntke et al., 2016).

Chapter 4: Effects of changing rainfall on litter decomposition by tropical millipedes and other invertebrates

M. J. M. Holle & O. T. Lewis, *Biotropica,* in review.

Author contribution

MJMH carried out the fieldwork, analysed the data, and wrote the manuscript. OTL provided suggestions and ideas on experimental design and commented on the manuscript.

Abstract

Climate change is expected to cause altered diversity and richness of invertebrate assemblages in tropical forests. However, little is known about the effects of these changes on ecosystem functions, and how altered biotic communities will perform under novel and extreme climatic conditions. Decomposition, facilitated by litter invertebrate macrofauna, is a key ecosystem function in forest ecosystems with relevance to soil fertility and crop yields in adjacent agricultural areas. We used mesocosm experiments to investigate how rates of decomposition mediated by invertebrates are likely to change under altered biotic and abiotic conditions arising from climate change. We investigated decomposition, soil nutrients, and crop seedling biomass when leaf litter was processed by millipedes (*Salpidobolus* sp.), alone and in combination with other litter invertebrates, and under ambient, elevated, and reduced-rainfall scenarios. In a separate set of experiments, we assessed how decomposition responds to millipede density. Decomposition increased significantly with rainfall, and diverse invertebrate assemblages including both millipedes and other litter invertebrates achieved the highest rates of decomposition. There was no evidence that the effects of altered rainfall on decomposition differed depending on the community of decomposers present. Seedlings planted into mesocosms where millipedes and other litter invertebrates occurred in combination achieved highest biomass, paralleling the results documented for litter decomposition, but these effects were not clearly associated with levels of soil phosphorus and nitrogen. The results highlight the importance of litter invertebrates, particularly *Salpidobolus* sp., and altered rainfall for decomposition dynamics in tropical forests, and the implications for plant growth.

Keywords: Tropical forest, Sulawesi, decomposition, land-use change, precipitation, millipede, litter invertebrate community.

Introduction

Alongside rapid deforestation (Geist & Lambin, 2002) and degradation due to agricultural activity (Balmford et al., 2012), climate change is expected to have pronounced

effects on tropical forest ecosystems. Predicted trends under climate change in tropical forest ecosystems include hotter and more variable temperatures and altered rainfall regimes (Bonal et al., 2016), including extremes of drought and high rainfall. These changes are expected to have marked effects on biodiversity as well the important ecosystem functions and services that it mediates (Lewis, 2009).

Decomposition is a key ecosystem function regulating soil fertility in both natural forests and in agricultural systems (Gray & Lewis, 2014; Power, 2010; W. Zhang et al., 2007), breaking up organic matter such as leaf litter and dead wood into smaller molecules that are available for plant growth, with benefits for forest regeneration (Contos et al., 2021; Santiago et al., 2012), and crop growth (Eisenhauer et al., 2018). Efficient decomposition is especially important in many tropical locations where soils typically have low fertility (Grau et al., 2017; Yeong et al., 2016).

Microbial decomposition is facilitated by detritivores such as litter-feeding invertebrates (Both et al., 2017; Culliney, 2013; Mohan, 2017; Power, 2010). Despite their likely importance for soil nutrient availability, litter macrofauna appear to be overlooked in current landscape management policies (Contos et al., 2021). Litter-dwelling fauna likely to be important in this context include earthworms, termites, woodlice and millipedes (David & Handa, 2010; Snyder & Hendrix, 2008). Millipedes (Diplopoda) are among the least studied groups ecologically, with most such research taking place in temperate ecosystems (Sierwald & Bond, 2007), and little data from tropical forests, where they reach their maximum diversity (Brewer et al., 2012). Millipedes are the third most diverse group of terrestrial arthropods (Kime & Golovatch, 2000), and have an important functional role in many ecosystems as effective detritivores (Kumar & Shakunthala, 2016; Sierwald & Bond, 2007; Smit & Van Aarde, 2001) consuming a wide variety of resources, especially leaf litter (Lawrence & Samways, 2003), in tropical areas (González et al., 2012). For example, the Seychelles giant millipede consumes an estimated 17.19% of daily litter fall, contributing significantly to nutrient cycling (Lawrence & Samways, 2003). Millipedes are also used as bioindicators because they have narrow tolerances and consequently respond rapidly to environmental change (Masse et al., 2017).

Despite evidence that climate change can affect decomposition rates via altered arthropod activity (Wu et al., 2021), the effects of climate change on ecosystem functions mediated by tropical forest millipedes are essentially unstudied. Furthermore, while the relationship between organismal density and rates of decomposition are well-established in other decomposer systems (e.g. Gotcha et al., 2022; Klemmer et al., 2012; Little et al., 2020), little

is known about how rates of decomposition change with millipede density. An experiment conducted by González et al., (2012) showed the significant influence of millipedes on leaf litter decomposition, but their importance relative to other litter invertebrates and their responses to changing environmental conditions remain unclear. To address these knowledge gaps, we investigated the functional contribution of millipedes and other invertebrates to litter decomposition under different rainfall regimes (dry, ambient, and wet) using mesocosm experiments. Similar approaches have been applied successfully to other invertebrate taxa (Manning et al.,2016; McGlynn & Poirson, 2012), and can help forecast the ecological effects of climate change (Fordham, 2015). We manipulated the composition of the leaf-litter invertebrate community (with millipedes excluded or included) and measured decomposition and other response variables related to decomposition (soil nutrients, seedling growth, and litter invertebrate community). In a supplementary experiment, we manipulated millipede density and measured litter decomposition. We hypothesised that (i) leaf litter decomposition would be significantly higher in the presence of millipedes; (ii) extremes of low and high precipitation would impair ecosystem functions mediated by millipedes and other litter invertebrates; and (iii) the effects of millipede density would differ under different environmental conditions. Given the absence of existing information on millipede-mediated decomposition and its sensitivity to climate change, we were further interested to test for potential synergistic effects between millipedes and other litter invertebrates in mediating decomposition, and whether these interactions were altered under elevated and reduced-rainfall scenarios.

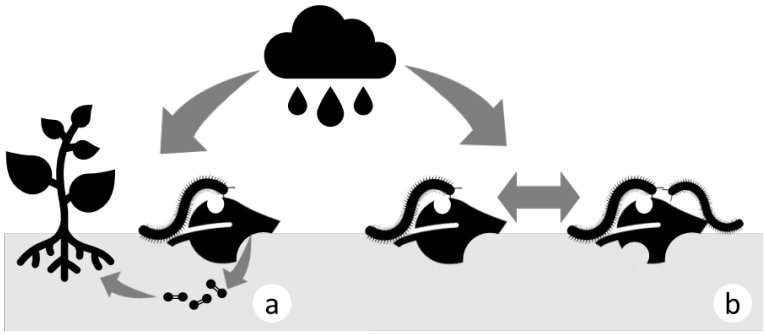


Figure 4.1. Visual summary of the two experiments investigating (a) effects of experimentally manipulated precipitation and community composition on decomposition, soil nutrients and seedling growth; and (b) effects of experimentally manipulated precipitation and varying millipede density on litter decomposition.

Methods

Study site and study system

The research was conducted in February 2020 in a shaded forest understorey location in Panua Nature Reserve (PNR) in the Pohuwato Regency (0° 31 59 N, 121° 49 30 E) of

Gorontalo Province, Sulawesi, Indonesia. Millipedes are a conspicuous and numerically dominant component of the macroinvertebrate community at this site (personal observation), perhaps reflecting availability of high-quality food (David & Handa, 2010). In particular, high densities of large-bodied *Salpidobolus* sp. millipedes (fig. 4.2.) make this an ideal location to investigate their functional role, interactions with other litter invertebrates, and responses to environmental change. While termites are widely considered to be major ecosystem engineers affecting cellulose decomposition and associated carbon cycling (Jouquet et al., 2011), field experiments using toilet rolls to quantify cellulose decomposition at our field site revealed a key role for millipedes. In the field, millipede abundance reached up to 88 individuals per 0.25 m^2 (unpublished data), and cellulose degradation was 25% higher when millipedes were present (initial field experiment, unpublished data).



Figure 4.2. Millipedes (*Salpidobolus* sp.) on the forest floor of Panua Nature Reserve, Sulawesi, 21 March 2020

Experimental enclosures and treatments

We manipulated invertebrate communities and rainfall levels within mesocosms formed from 20 cm-diameter plastic flowerpots. Mesocosms were filled to a depth of 8 cm with soil collected from nearby forest and supplied with dried leaf litter as a substrate for decomposer activity. Soils were dried by leaving them under direct sunlight exposure for two days before starting the experiment so that soil humidity could be adjusted experimentally. Mesocosm bases were sealed with fine nylon mesh to prevent macro-invertebrates entering or leaving while allowing water to drain. The tops of mesocosms were also covered with fine mesh to prevent litter or macrofauna entering while allowing air to circulate.

Individual mesocosms were allocated to one of two invertebrate community treatments, each with two levels, in factorial combination: millipedes (present/absent) and other litter invertebrates (present/absent). For simplicity we use the term "litter invertebrates" to refer to litter-dwelling invertebrates other than millipedes. Millipedes and litter invertebrates were included at natural densities. To standardise the experiments, all millipedes used were in the 2.75-3.25 gram body mass range with 4 millipedes added to each mesocosm, within the range of millipede densities observed in the field. Mesocosms were further allocated one of three initial rainfall treatments to simulate different climate change scenarios, corresponding to soil water content of <3%, 10-15%, and >22% water as measured using a digital soil moisture meter, representing dry, ambient, and wet soil respectively. There were 6 replicates of each treatment combination, making 72 mesocosms in total (4 invertebrate treatment combinations x 3 rainfall treatment levels x 6 replicates).

To achieve rainfall treatments, water was poured evenly across the surface of the mesocosm until the desired soil moisture content was achieved. Consistently adding 50, 100, or 200 ml of water every second day achieved the desired soil moisture content of <3%, 10-15%, or >22%. A transparent plastic rain shelter was erected 2 m above the mescosoms to prevent water input from precipitation while maintaining near-natural daylight conditions.

As a substrate for decomposition, we added leaves of *Macaranga* sp., pioneer trees which have been used previously in similar studies (Chellaiah & Yule, 2018; Plowman & Ewers, 2012). Collected leaves were exposed in direct sunshine for 3 days until completely dry. Larger dried leaves were broken up by hand into fragments of approximately 25 to 40 cm^2. Samples weighing 5 g were sealed within 10x15 cm non-decomposable coarse-meshed nylon litterbags (0.5 cm mesh size) using rust-proof clips and placed on the soil surface within each mesoscosm.

To seed mesocosms with a natural invertebrate community we exposed filled litter bags on the forest floor for 1 week to allow colonisation. For treatments including (non-millipede) litter invertebrates, the bags were then transferred directly into the mesocosms. Treatments without litter invertebrates were subjected to a further one-day drying in full sunlight to kill litter invertebrates, before being transferred into mesocosms. The litter bags for invertebrate exclusion treatments were filled one day earlier than those with invertebrates, allowing the experiment to start at the same time for all treatments. Experiments were terminated after 7 days when at least one replicate had leaf litter almost completely decomposed.

Data collection

We collected data on litter decomposition rates, soil nutrients, and growth of seedlings from seeds planted into mesocosms after the termination of the experiment. After termination of the mesocosm experiment, to measure decomposition we carefully removed the remaining litter from each litter bag and separated out any soil particles. The litter was then dried in direct sunshine until completely dry and weighed to the nearest 0.05 g using a digital balance.

Soil samples from each mesocosm were collected and dried in direct sunlight to prevent further biological activity. After aggregating soils from pairs of mesocosms from each treatment combination (n=36), soil chemistry was assessed at the Institute for Agricultural Technology Studies (BPTP), Yogyakarta, Indonesia. Total nitrogen was assessed using the Kjeldahl method (Bremner, 1960), and total phosphorus was extracted with basic oxide followed by spectrophotometer measurement (Liu et al., 2014).

A seedling planting experiment was performed to investigate whether altered nutrient cycling provided by millipedes affects seedling growth (Brearley et al., 2003). Six seeds of maize (*Zea mays* L.*),* the main crop in adjacent agricultural farmland, were planted into each mesocosm after termination of the millipede exclusion experiment. Growing seedlings were watered (200 ml of every second day for 2 weeks), and then harvested and separated into aboveground and belowground parts. Dry biomass of the aboveground part was measured after drying seedlings to constant mass in direct sunlight.

Effects of millipede density on litter consumption

In a supplementary mesocosm experiment we varied numbers of millipede individuals under three experimental rainfall treatments, with and without litter invertebrates. Mesocosms design and substrate preparation was as described above. Treatments with 0, 1, 3, and 5 millipede individuals were established, either with or without other litter invertebrates. Each treatment combination had 2 replicates, making 48 mesocosms in total. Pots were watered every two days with 40, 75, and 150 ml of water for dry, ambient, and wet treatments, respectively. The volume of water used differed slightly from the first experiment because the mesocosm set up was placed under a non-transparent roof where evaporation from the soil was lower, so that soil moisture could be maintained at the desired level with lower water addition. The experiment was terminated on the sixth day when leaf litter had almost completely decomposed in at least one replicate.

Data analysis

Statistical analyses and data visualisation were performed using R (R Core Team, 2020). The effects of rainfall treatment, invertebrate presence and millipede presence and their interactions on litter decomposition, crop seedling biomass, and soil nutrient (N total and P total) were analysed with general linear models (using the *glm* function). Full models with interactions were fitted, and then non-significant interaction terms dropped from the model until the minimal adequate model was obtained according to the AIC scores. To identify the specific groups that were significantly different, GLM analysis was followed by a post-hoc analysis with a Tukey Contrasts test using the *glht* function in the *multcomp* package in R. Data were visualised using the *ggplot* function of the *ggplot2* package. Data in the second experiment with varying millipede numbers were analysed using the same approach as the first experiment. In this analysis, data from the two macrofauna community composition treatments (I: Invertebrates only; IM: Invertebrates and millipedes in combination) were combined as these treatments did not differ significantly.

Results

Effects of the rainfall treatments and community composition on litter consumption, seedling biomass, and soil nutrients

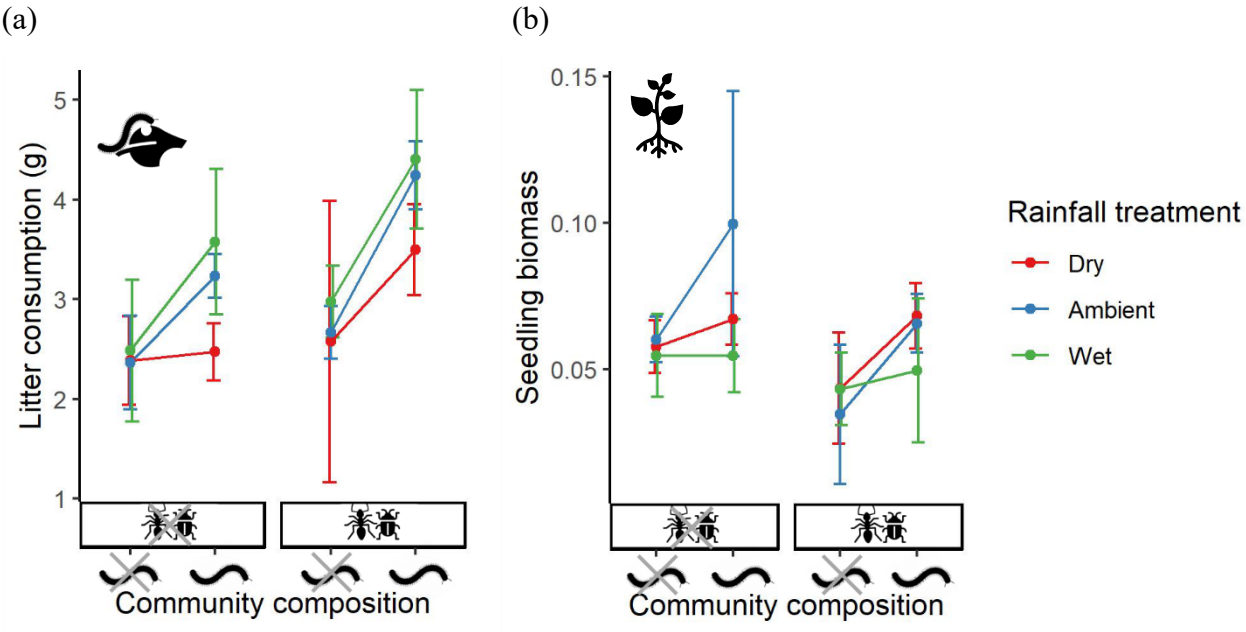


Figure 4.3. Effects of macrofauna communities on decomposition (a) and seedling biomass (b) under different rainfall levels. Error bars show standard errors of the mean.

In the analysis of the effects of macrofauna communities and rainfall treatment on decomposition, the best model as judged by AIC included the millipede x invertebrate interaction ($F_{1,66}$=4.57, p=0.036). Millipedes tended to increase litter consumption to a greater

extent when invertebrates were present (fig. 4.3.a). Litter decomposition differed significantly among rainfall treatments ($F_{2,66}$=6.305, p=0.003) and was significantly lower under dry conditions than wet conditions (p=0.002, Tukey contrasts). There was no significant rainfall x invertebrate treatment interaction.

The best model as judged by AIC included the interaction between millipede and invertebrate presence, although the interaction effect judged on its own was not statistically significant ($F_{1,66}$=0.201, p=0.655; fig. 4.3.b). Seedling biomass was significantly higher in the presence of millipedes ($F_{1,66}$=14.39, p<0.001) but significantly lower in the presence of other invertebrates ($F_{1,66}$=9.27, p=0.003). There was no significant interaction effect involving rainfall treatments, and a trend towards low seedling mass in the high rainfall treatment ($F_{2,66}$=2.965, p=0.058).

Principal Component Analysis (PCA) scores for soil chemistry of samples from the different treatments did not form distinctive clusters (fig. 4.4.). The first and second principal components accounted for 35.79% and 32.38% of the total variance in soil nutrients, respectively.

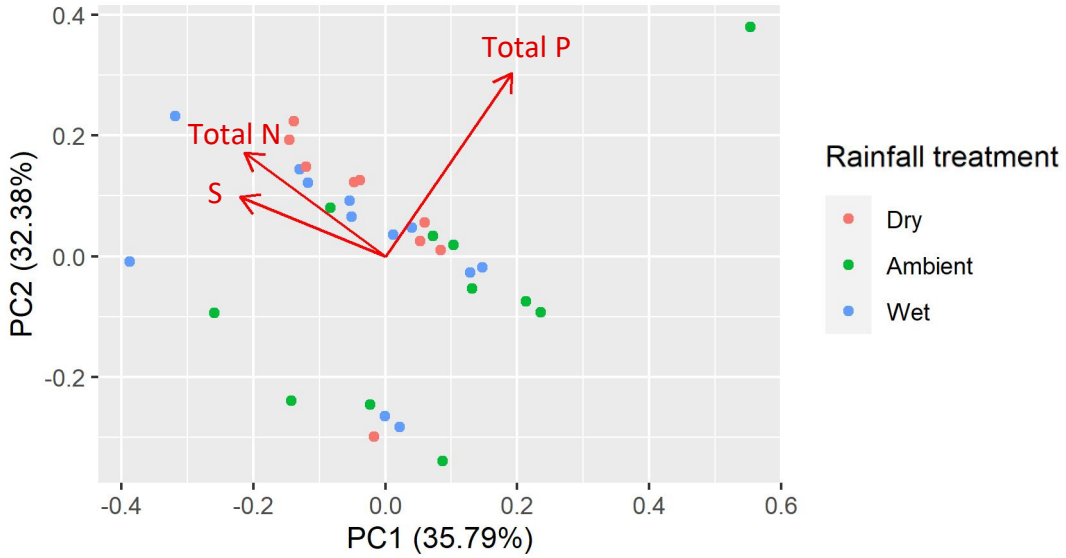


Figure 4.4. Biplot of principal component analysis (PCA) of soil nutrient parameters (Total N, total P, and S) across different rainfall levels. Rainfall treatments are represented by different colours. Vectors represent loadings of soil nutrient variables.

Effects of millipede density and rainfall treatments on litter consumption

A model including the millipede density x rainfall treatment interaction had the lowest AIC value ($F_{6,24}$=12.008, p<0.001). Millipedes tended to increase litter decomposition to a greater extent as rainfall increased, with the low-rainfall scenario in particular reducing the positive effects of millipede numbers on litter consumption (fig. 5.4.). Other main effects

(Litter invertebrate presence: $F_{1,24}$=0.416, p=0.525) and interactions (Community composition x water treatment: $F_{2,24}$=2.206, p=0.132; Community composition x number of millipede individuals: $F_{3,24}$=1.288, p=0.301; Community composition x water treatment x number of millipede individuals: $F_{6,24}$=1.750, p=0.153) were non-significant.

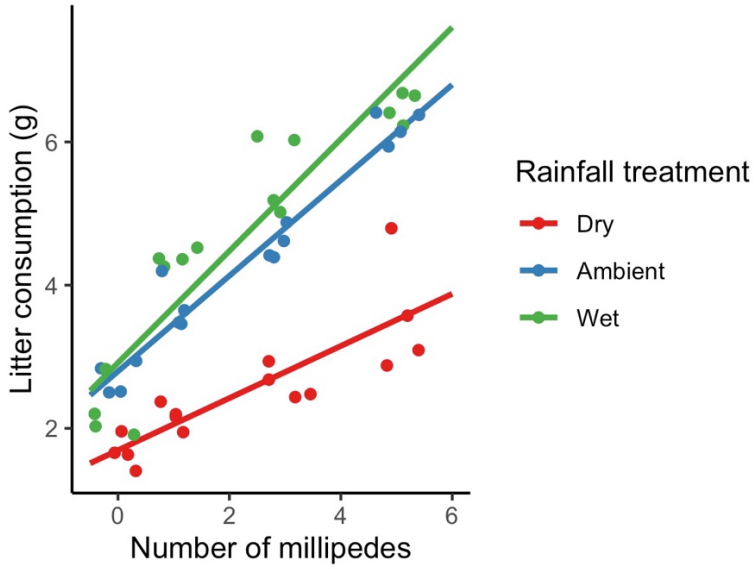


Figure 5.4. Litter consumption by varying numbers of millipede individuals under different experimental rainfall treatments. Data from the two macrofauna community composition treatments (Invertebrates only vs Invertebrates and millipedes in combination) are combined as these treatments did not differ significantly. Data points are jittered to avoid overlaps.

Discussion

Changing rainfall influenced litter consumption mediated by millipedes and litter invertebrates. Both litter consumption and crop seedling biomass were promoted by the presence of millipedes alongside other litter invertebrates. Drought conditions tended to reduce decomposition and lowered the extent to which decomposition increased with millipede abundance. There was little evidence that millipedes and other litter invertebrates competed for shared litter resources; in fact, there was evidence of synergistic effects on decomposition.

Millipede and litter invertebrates synergistically influence litter decomposition

Our results show that the effects of millipedes on litter consumption increased in the presence of other invertebrates. While studies on the facilitative interactions between millipedes and other litter invertebrates are lacking in the tropics, these have been documented in other ecosystems. In European beech woods, earthworm biomass increased in the treatments with millipedes (*Glomeris marginata*) and *vice versa*, presumably because of the provision of food in the form of faecal material (Bonkowski et al., 1998). *Glomeris marginata* returns 90%

of ingested leaf litter to the soil as faecal pellets in temperate deciduous forests (van der Drift, 1975).

By converting litter into faeces, millipedes contribute to accelerating organic matter turnover and thereby enhance carbon cycling (Joly et al., 2020). In a Mediterranean forest, millipedes and snails complementarily decompose freshly fallen leaf litter (de Oliveira et al., 2010). Synergistic interactions between millipedes and other invertebrates can be driven by resource partitioning and facilitation (de Oliveira et al., 2010), potentially leading to positive Biodiversity-Ecosystem Function (BEF) relationships.

Decomposition increases less rapidly under drought condition.

In general, we found that experimental droughting inhibited litter decomposition whereas litter decomposition was maintained under wetter conditions. This pattern is consistent with studies showing that drought has detrimental impacts on soil microorganism and invertebrate activity, including decomposition (e.g., (Palmia et al., 2019; Siebert et al., 2019; Xie et al., 2020). Moreover, droughting might reduce the facilitative effects of millipedes on microbial decomposition, via their tendency to increase the surface area for microbial action (Ruan et al., 2005). Droughting might therefore alter invertebrate-provisioned litter decomposition both directly and indirectly via altered activity of microorganisms. Despite having a significant effect on litter decomposition as a main effect, rainfall treatments did not interact significantly with the presence of either millipedes or other litter invertebrates, meaning that the changes of precipitation level do not significantly extend or reduce litter decomposition along with changes in invertebrate abundance.

In the absence of millipedes and litter invertebrates, microorganisms, particularly fungi, are expected to degrade leaf litter. In contrast to previous studies (Allison et al., 2013), decomposition in the absence of millipedes and litter invertebrates did not alter across different rainfall regimes. Direct effects on microbial activity can therefore be ruled out as a cause of altered decomposition under dry conditions.

In contrast to the effects of experimental droughting, decomposition under our high-rainfall treatment was comparable to that under ambient conditions (fig. 5.3.a). While high-moisture scenarios can reduce invertebrate contributions to plant organic matter decomposition (Ulyshen, 2014), high rainfall extremes leading to periodic flooding have been found to increase decomposition (Day, 1983; Padial & Thomaz, 2006) by increasing moisture aboveground and anoxic conditions belowground (Neckles & Neill, 1994) and by boosting microbial decomposition through aeration (Battle & Golladay, 2001).

In our experiment, treatments including only non-millipede litter invertebrates had similar litter consumption activity to the control treatment without litter invertebrates. The relatively short duration of litter exposure to colonisation and the experimental period of less than two weeks may not have allowed for full litter invertebrate colonisation and activity, while sufficing for non-invertebrate decomposers such as fungi and microbes. In future work it would be helpful to evaluate the colonisation rates as well as decomposition rate of decomposer groups.

Although the effects of the leaf litter species diversity on the decomposition was not investigated in this study, there is a possibility that millipede-mediated decomposition will be higher when more diverse plant species are represented within the leaf litter. Litter sources are highly heterogeneous under natural conditions on the tropical forest floor and millipede litter consumption can be greater when litter sources are diversified (Ashwini & Sridhar, 2005). In addition, previous research has shown that both litter quality and litter diversity have a significant impact on litter decomposition (Getaneh et al., 2022). Data recorded in our study, which used only one type of leaf litter, might underestimate millipede-mediated litter consumption. Therefore, along with ensuring that litter invertebrate communities are thriving in the ecosystem, managing vegetation diversity might maintain nutrient turn-over and preserve ecosystem services, in this case the nutrient cycle, mediated by litter invertebrates (Isbell et al., 2011).

In a mesocosm experiment that tested the effects of soil moisture levels and the number of millipede individuals on litter consumption (fig. 4.7.), we discovered that litter consumption improves in wetter conditions, indicating that wetter conditions provide a favourable environment for millipede decomposition activity (Frith & Frith, 1990). However, an excessive wet environment that results in flooded soil may impair millipede activity because it alters the biological activities of other soil invertebrates. For example a study by Roeder et al., (2018) found that the invertebrate community decreased by 93% in abundance, 60% in species richness, and 64% in biomass nine months after flooding occurred. In the current study there was little evidence that millipedes are competing for limiting resource, as indicated by decomposition improvement with increasing number of millipede individuals in the mesocosm system, at least until the millipede densities reached five millipedes per flower pot, equivalent to 127 individuals/m^2. Experiments using even higher millipede densities and over more extended periods would be needed to provide a clearer understanding of the relationship between millipede densities and decomposition rates. When millipedes were absent, both

wetter and drier soil environments had poorer litter decomposition than the ambient soil state, demonstrating that decomposition is altered in extreme precipitation scenarios.

Nutrient released from decomposition affect crop seedling biomass but have idiosyncratic effects on soil nutrients

From the results shown in figure 4.3.b, we found that simulated rainfall variations affected seedling biomass. The absence of interaction effects indicates that the effects of rainfall treatment and presence of litter invertebrates on seedling biomass were additive, with higher seedling biomass in the wetter condition and in the presence of millipedes and litter invertebrates being no more than the sum of its main effects. While litter breakdown was greater in wetter conditions, seedling biomass was higher in drought conditions. This contrasts with prior research that found decomposition to be a limiting factor for tree seedling growth (Santiago et al., 2012) and crop growth (Eisenhauer et al., 2018). We propose three possible explanations for the results: (1) sufficient water content in all rainfall variation treatments, (2) the presence of confounding factors, and (3) soil nutrient availability prior to the experiment.

Seed requirements for breaking dormancy are species specific, but this generally needs a specific water and temperature conditions (Soltani et al., 2022), but not specific soil nutrient conditions. It is probable that water availability in the drought treatment was sufficient to break dormancy, so that seed germination across rainfall treatments began at roughly the same time. The subsequent phase of seedling development is increasingly dependent on soil nutrients and other external conditions. Soil nutrients are not the only factors limiting seedling growth. In addition to soil nutrients, soil temperatures are a crucial environmental component related to root and shoot growth (Xia et al., 2021). The optimal temperature for maize seedling growth is 20°C , while the optimal temperature range for seed germination is between 20°C and 35°C (Khaeim et al., 2022). Our experiment was conducted at temperatures within this range, which allowed for optimal seedling germination and growth. Therefore, water availability and air temperature may not be responsible for the opposite pattern of seedling biomass and decomposition observed. Therefore, it is possible that the soil within our mesocosms may have already had sufficient nutrients for plant growth in advance of the experiment. Ideally, measurement and monitoring of the nutrient status of the soil over the course of the experiment would have allowed the extent of soil nutrient enrichment resulting from decomposition activity to be quantified.

Intriguingly, the presence of millipedes and other invertebrates had opposing impacts on seedling biomass, with millipedes having a positive influence and other invertebrates having

a negative one. Even though numerous studies have indicated a positive influence of litter decomposition on seedling biomass, decomposing litter can also have neutral or negative effects on seedling development (Coq et al., 2012). This contradictory effect may be caused by two mechanisms: plant-microbe competition for soil nutrients, or secondary compound inhibition of nutrient uptake. Seedlings share nutrient resources with soil microbes, reducing the net benefit to seedlings from the soil nutrient provided by litter decomposition. Secondary compounds released by decomposition may limit plant N uptake. It is therefore possible that decomposition by millipedes and other litter invertebrates results in the release of chemicals that affect seedling nutrient uptake and growth performance. This could be investigated further by comparing the secondary compounds produced by millipedes and litter invertebrates and examining the effects of these compounds on seedling growth performance.

From the standpoint of applied ecology, forest canopy loss and habitat alteration that may reduce millipede density (Chapter 5) could indirectly reduce decomposition and thus lower soil fertility. In an agricultural context, such effects can lead to farmers relying on substantial fertiliser input to maintain agricultural productivity. Alternative solutions to boost millipede-mediated activity could include maintaining ground-level refuges that provide shade for millipedes while permitting the growth of shade-intolerant crops such as maize. While allowing sun-loving plants, such as maize, to keep out of shade, mulching with organic matter may not only serve as a refuge, but also as a source of organic matter for the decomposition process (Ngosong et al., 2019). It has been demonstrated that organic matter applied to maize plants results in a crop yield comparable to that of maize grown according to standard agricultural practises (Appendix fig a.4.).

While soil nutrients did not respond measurably to experimental rainfall treatments in our experiment, dry conditions can under some circumstances dramatically reduce the release of both nitrogen and phosphorus (Xie et al., 2020). Studies from tropical forests that investigate nutrient release from decomposition under varying soil moisture conditions are lacking, especially those investigating increased-moisture (rather than droughting) conditions. Therefore, further study that integrate numerous predictors, such as temporal changes, litter type, and more comprehensive soil nutrients and leaf chemical compounds, could explain nutrient release processes under environmental change and community composition variation.

Decomposition rates respond more slowly to increased millipede densities under drought conditions

While litter consumption increased as millipede numbers increased, litter consumption was noticeably lower, and increased more slowly with millipede density, under dry conditions. Litter consumption did not increase with rainfall in the absence of millipedes, probably due to altered litter consumption activity by non-millipede decomposers (i.e. microbes). Experiments that include higher (but nonetheless realistic) millipede densities, and under more extreme wet conditions would be needed to clarify any effects of intraspecific competition and how these might be affected by environmental change.

Conclusion

Our results highlighted that altered precipitation regimes and community assemblages can affect litter invertebrate decomposition activity, with consequences for plant growth. In particular, drought but not elevated rainfall led to reduced decomposition. Decomposition in our study was facilitated by a more diverse community assemblage including both millipedes and other litter invertebrates. The results of this study are relevant to natural management of soil fertility, suggesting the likely importance of creating or preserving habitats that will support a diverse litter invertebrate community. Such approaches could help maintain ecosystem functions in the face of changing environmental conditions in human-modified tropical landscapes. Further assessment of the effects of habitat modification, changes to precipitation and other climatic variables, and shifts in community assemblages, are now needed for diverse ecosystem functions mediated by a wide range taxonomic group, to provide a more comprehensive understanding of the functional impacts of environmental change in the tropics.

Chapter 5: Tropical forest fragments idiosyncratically contribute ecosystem functions to adjacent small-holder maize farmland.

M. J. M. Holle & O. T. Lewis, *in preparation for submission.*

Author contribution

MJMH carried out the fieldwork, analysed the data, and wrote the manuscript. OTL provided suggestions and ideas on experimental design and commented on the manuscripts.

Abstract

Most farmers in tropical region are small-holders, who rely on forest patches and trees in agricultural landscapes. Small-holder farmers who grow seasonal crops often experience crop failures due to soil infertility and pest attack, increasing their economic vulnerability. At the same time, agricultural land might be benefitted by ecosystem services tropical forests offer. Tropical forests adjacent to agricultural areas can export ecosystem services such as decomposition and predator-mediated biological pest control. In Sulawesi, Indonesia, we evaluated the potential of the spillover of the decomposition and insect herbivore (possible pest) predation from forests to the maize farmland. We used cellulose baits (toilet rolls) and model plasticine caterpillars to assess decomposition and predation along transects ranging from forest to maize farmland. In addition, we measured soil bulk density and millipede density at the same sampling points with the decomposition assessment. We observed that decomposition in sampling points closer to the forest did not differ from that in sample points further away from the forest, showing that there was no decomposition spillover. However, predation was substantially higher near the forest sampling points, indicating that predation of insect herbivores is transferred from the forest to the maize farmland. Our findings indicate that predation of insect pests within crops, but not decomposition, is likely to be forest-dependent. Thereby, potential pest control service might provide an incentive for forest conservation efforts in human-modified tropical environments. However, whether predator and pest predation services spilled over from forests are sufficient to restrict pest outbreaks requires further investigation to inform agriculture and conservation strategies.

Keywords: Small-holder farm, tropical forest, Sulawesi, decomposition, predation, herbivorous insect, spill-over.

Introduction

Many smallholder farmers in tropical regions rely on forest patches and trees in agricultural landscapes (Ango et al., 2014). Agricultural growth and intensification, on the

other hand, constitute a significant risk to tropical forests (Carrasco et al., 2017; Gibbs et al., 2010), with about 6 million hectares of tropical forests currently converted for agricultural purposes (Mayaux et al., 2005). At the same time, forest conversion to agricultural land has been shown to reduce important ecosystem functions such as soil fertility (Holle & Lewis, 2022; Chapter 2) and insect management (Chapter 3). Given that rainforest biodiversity provides these services (Lewis, 2009), effectively managing human-modified landscapes, including areas where agroecosystems and tropical forests coexist (Gardner et al., 2009), and integrating management for ecosystem functions into land-use planning (Power, 2010) are essential for long-term sustainability and improved social welfare (Harvey et al., 2008).

As sustaining ecosystem integrity in the tropical region is one of the most pressing problems in conservation biology (Brawn, 2017), diversifying crops, for example through polyculture or agroforestry, is widely suggested as a potential solution to maintain ecosystem function integrity while producing adequate food (Scherr & McNeely, 2007). However, these agricultural approaches are less suitable to seasonal crops. In some cases, agroforestry actually reduces crop yields because a higher agroforestry layer reduces sunlight, which is required for sun-tolerant seasonal crops while competing for soil moisture (Simpson, 1999), discouraging farmers from implementing this system because agriculture profitability is the most common motivation for farmers to implement specific farming practises (Rois-Díaz et al., 2018). Farmers instead tend to utilise non-sustainable practises, such as fertiliser and insecticide, because sustainable agriculture is a complicated long-term process (Schader et al., 2016). Simultaneously, important crops - maize, rice, soy, and wheat, which are seasonal crops - supply two-thirds of global food calories (Kim et al., 2019), emphasising the need for crop sustainability. Annual crops are more prone to crop failure than perennial crops (Crews et al., 2018), preventing natural ecosystem services from being incorporated into crop production.

Some of the causes of economic loss due to crop failures in seasonal monoculture are soil degradation and pests or weeds (Crews et al., 2018). Species-poor monoculture plantation communities are especially susceptible to fertility depletion (Ewel et al., 1991). Given that soil fertility is maintained by efficient nutrient cycling that relies on decomposition processes (Gray & Lewis, 2014; Power, 2010; W. Zhang et al., 2007), ensuring that this process takes place and is well maintained is important to minimise the risk of fertility depletion. Climate and biotic factors, such as the activity of decomposer communities (including earthworms, termites, and other litter invertebrates), influence the decomposition of organic matter, such as leaf litter and wood (Both et al., 2017; Mohan, 2017; Power, 2010).

Similarly, the loss of natural enemies of pests reduces yields in many of the most important tropical crops (Oliveira et al., 2014). These agricultural pests can frequently be reduced naturally by top-down control from predators as an alternative to high-input and often environmentally harmful chemicals (Zhang & Adams, 2011). Natural enemies such as predators, parasitoids, and pathogens are used in pest control services (Power, 2010; Tscharntke et al., 2005), with arthropods and mammals dominating insect herbivore predation in tropical agriculture (Denan et al., 2020).

Here, we investigate whether ecosystem functions mediated by invertebrates are transferred from forest fragments to nearby agricultural land. As biodiversity conservation in agricultural landscape should be adapted to the farmer's needs (Norgrove & Beck, 2016), we focus on ecosystem functions that are beneficial for both forest regeneration and agricultural production: decomposition and predation of herbivorous insects. These functions support soil fertility and pest-control services, respectively. Our focal landscape is a mosaic of patches of tropical forest and smallholder maize farmland in the province of Gorontalo, Sulawesi, Indonesia. Together with soybeans, maize expanded the greatest in absolute area compared to other tropically-planted crops from 1999 to 2008 (Phalan et al., 2013). Although most farms are small and family-operated (Lowder et al., 2016), most research has concentrated on large-scale industrial agriculture (Reiss-Woolever et al., 2021), ignoring the efforts of seasonal smallholder agriculture to preserve ecosystem services. Maintaining the integrity of ecosystem functions in smallholder monoculture is crucial because the initial step in forest conversion is often rural farmers converting intact forests to small holder agriculture (López-Carr, 2021), especially in tropical forests, which have a rich diversity of ecosystem functions (Brandon, 2014).

We studied decomposition and predation of caterpillars along transects at the transition from forest to farmland. We hypothesised that (i) decomposition and predation of caterpillars decline with distance from forest, and (ii) predation of caterpillars has greater spillover than decomposition. Understanding the contribution of forest fragments to small-holder agriculture is critical for both forest conservation and the sustainability of rural livelihoods, as both should be inclusive (López-Carr, 2021)

Methods

Study site

The project was carried out in the Panua Nature Reserve (PNR), which was situated in the Pohuwato Regency (0° 31 59 N, 121° 49 30 E), Gorontalo Province, Sulawesi, Indonesia

during the rainy season (January-March 2020). This protected area is under threat from forest conversion into agricultural land and mining, and illegal logging by local people living adjacent to the nature reserve. The research was conducted in forest and adjacent maize farmland near the edge of the nature reserve to investigate if forest fragments are contributing functionally to the nearby farmland. Forest sites had experienced low-intensity selective logging of large and emergent trees, but retained closed-canopy structure. Maize farmland sites are managed by smallholder farmers within and right on the edge of the nature reserve. Sampling in the maize fields was started three weeks after planting, when maize stalks started to create locally-shaded microclimates. Maize farmland is a non-permanent land use: outside of the planting season (mostly the wet season), fallow maize farmland can develop into either shrubland, bare ground, or grassland.

Eight line transects were established running from the forest edge into the maize farmland, with sampling sites within the forest (-10 m, -5 m) at the forest edge (0 m), and in the corn farmland (5 m, 10 m, 15 m, and 30 m). At each sampling site, decomposition rate, millipede abundance, herbivore predation, soil bulk density, air temperature and air humidity were recorded. Data on decomposition (only) were additionally collected at 20 m.

Quantifying decomposition and related parameters

Decomposition occurs not just on the fallen leaves of trees, but also on the plant's woody portions. As a standardised lignin (woody) substrate that has been confirmed to be ingested by millipedes, cellulose baits (single ply, unscented coreless toilet rolls) were used to evaluate millipede consumption activity between February and March 2020 (Leitner et al., 2018). Three 5 g toilet rolls were set up in 7 line transects at each site, for a total of 147 (31 of them were not discoverable) toilet rolls (7 transect lines x 7 distance variations x 3 toilet rolls) used in the experiment. After two weeks, the remaining toilet rolls were collected, cleaned, sun dried, and weighed to determine the cellulose consumption rate.

Along with decomposition measurements, two other decomposition-related factors are decomposer abundance and soil bulk density. Given that millipedes, *Salpidobolus* sp., are the largest component of the decomposer community at the research site (Chapter 4), we concentrated on estimating millipede abundance. Millipede abundance was evaluated by counting millipedes using 1x1m quadrat plots, randomly located in three distinct sites more than 2 meters apart at each sampling site (within 15 meters of where decomposition was measured and under similar vegetation and topographical conditions). To estimate millipede densities, counts were taken on cloudy days following rain events the previous day. As the

abundance estimation varied greatly depending on the environmental condition, the estimation was performed multiple times. Data analysed were for the highest recorded abundance as this is assumed to record closest to the realistic abundance where millipedes were visible on the ground. Under these humid conditions, millipedes tend to crawl on the soil surface, whereas millipedes are often hidden belowground otherwise (personal observation). Furthermore, because long-term organic matter removal affects soil bulk density (Sayer, 2006), we assessed soil bulk density by collecting 6 cm depth soil samples at each sampling site with a modified soil sampler composed of 5 cm diameter PVC tubing. Soil samples were dried and weighted in the sun, allowing soil density to be calculated by dividing soil volume by soil dry mass.

Predation of caterpillars variability across distance

Plasticine caterpillars are commonly used to evaluate insect herbivore predation (Howe et al., 2009; Nurdiansyah et al., 2016; Denan et al., 2020), which reflects pest control services (Barbaro et al., 2017). Plasticine caterpillars were used to estimate predation rates from predators such as arthropods, birds, reptiles, and mammals. Herbivorous insects were represented using non-toxic plasticine modelling clay (Newplast light green) shaped in the form of caterpillars. Plasticine caterpillars were created by rolling modelling clay on a flat surface and cutting it into 3 mm wide by 15 mm long pieces. The plasticine caterpillars were shaped like 'inchworm' (family Geometridae) caterpillars. Ten plasticine caterpillars were attached using UHU super glue to the upper surface of ten plant individuals (either maize individuals or plant seedlings and shrubs) 1.5 m above the ground and left for two days. Seven linear transects were established, ranging in length from 10 m in the forest to 30 m in the maize farming. Three replicates of ten caterpillars were deployed at each of seven places relative to the forest edge: -10 m, -5 m, 0 m, 5 m, 10 m, 15 m, and 30 m (10 caterpillars x 3 replicates x 7 distances x 7 transects). The total number of plasticine caterpillars utilised in this study was 1440 because they were not placed at the 30 m distance on one of the transects.

Plasticine caterpillars were left in position for two days and then recovered to score for predator damage. Where caterpillars were missing the ground was searched to check for caterpillars that had fallen from the vegetation. Plasticine caterpillars recollected from the vegetation and the ground are included in the analyses. After being collected, all caterpillars were sorted based on the presence and type of bite marks. Where there was doubt about the identity of the predator, the bite marks were identified and photographed. Bite marks were recognised using bite-mark identification guidelines based on predator research conducted

throughout the Asia-Pacific region (Australia, Papua New Guinea, and the Philippines) (Low et al., 2014).

Data analysis

All statistical analyses and graph visualization were performed using R (R Core Team, 2020). The effects of distances from the forest edge on the response variables were investigated using mixed effects models (using the *lme* function in the *lme4* package), with distance as a continuous explanatory factor and transect as a random effect. Individual response variables evaluated included cellulose consumption, predation of caterpillars, millipede abundance, and soil bulk density. As a two-column response variable for predation of caterpillars, we used combination attacked and non-attacked (binomial errors). The data analysis was carried out separately in two different sets: forest data points and maize farmland data points. Data points at the forest edge (0 m) were included with the forest data points. The data from maize farmland data points were analysed to investigate the impacts of distance from the forest edge on predation of caterpillars. Figures shows all data points from the forest to the maize field sites.

Decomposition, decomposition-related parameters, and predation of caterpillars showed varied trends with distance relative to the forest edge. There was no significant trend in cellulose decomposition with distance from the forest edge within the maize farmland ($F_{1,51}$=0.5002, p=0.4826), but in the subset of forest data points, there was a significant decrease in decomposition with distance from the forest edge into the forest interior ($F_{1,48}$=9.042, p=0.0042). Millipedes were recorded only in the forest. Within the subset of forest data points, we found that millipedes abundance declined towards the forest edge ($F_{1,39}$=19.203, p<0.0001). Soil density was close to being significant to distance for forest ($F_{1,52}$=3.97, p=0.051) but was not related within maize farmland ($F_{1,70}$=1.30, p=0.258) data points.

For the predation of caterpillars data, we referred to the data that has been described in Chapter 3. We recovered 1377 of 1440 caterpillars (95.62%) in total of which 681 (49.5%) were predated. Unlike decomposition, predation of caterpillars declined with distance into the maize farmland from the forest fragments ($F_{1,73}$=5.6004, p=0.0206). The proportion of attacked caterpillars at -10 m, -5 m, 0 m, 5 m, 10 m, 15 m, and 30 m were 66.7%, 73.1%, 60.6%, 37.9%, 37.9%, 40.90%, and 25.9% respectively. In a separate analysis, attack rates were not related to distance in the subset of forest data points (-10, -5, and 0 m from the forest edge; $F_{1,55}$=2.4, p=0.127). All predators that attacked plasticine caterpillars were invertebrates, especially ants (Hymenoptera).

Results

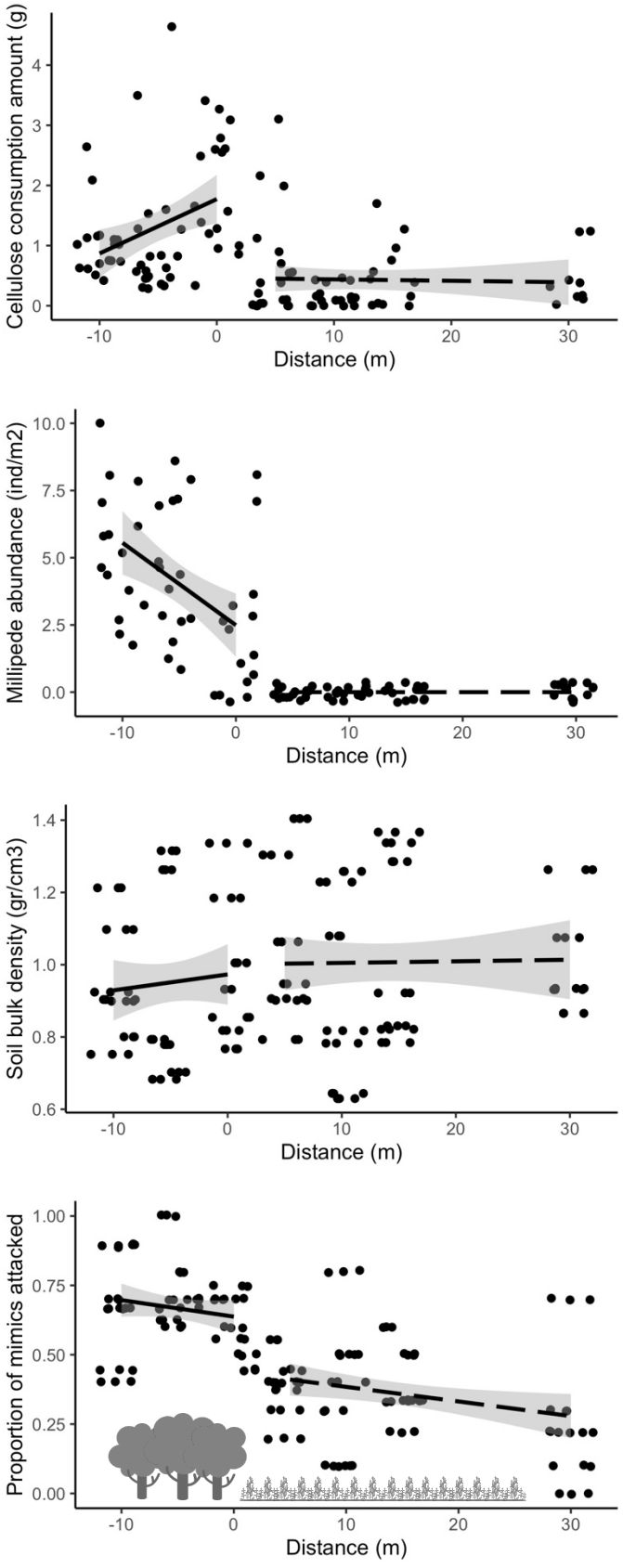


Figure 5.1. Ecosystem functions and associated parameters in relation to distance from the forest edge (n=7 transects). a: Cellulose decomposition; b: millipede abundance; c: soil bulk density; and d: predation of caterpillars. Data points are jittered to avoid points overlapping. Grey shading represents the 95% confidence interval for predictions from a linear model. Solid and dashed lines represent linear regressions for datapoints in the forest solely and maize farmland only, respectively. Figure (d) is adapted from Chapter 4.

Discussion

The ecosystem functions and associated parameters investigated exhibited different with distance from forest into farmland. In general, decomposition and its associated characteristics did not appear to rely on forest fragments, as evidenced by the lack of a declining trend in decomposition as one moved closer to the maize farmland. However, predation of caterpillars was forest dependent, with plasticine caterpillars being more likely to be predated at closer proximity to forest fragments.

Forest fragments spillover predation of caterpillars but not decomposition

Tropical forest fragments can spillover their biodiversity to less diverse agricultural land nearby (Lucey & Hill, 2012). This leads to the expectation that ecosystem functions will also be transferred as the concept of biodiversity-ecosystem functioning (BEF) strongly links these two components (Hong et al., 2022). Although forest conversion to maize farmland is likely to alter litter decomposition (Attignon et al., 2004; Holle & Lewis, 2022 (Chapter 2); Kagezi et al., 2016), cellulose decomposition did not change significantly with distance either in the forest or in the maize farmland (fig. 1), indicating that decomposition is not transferred from forest to nearby farmland. Previous research in East African coastal forest landscapes discovered a similar trend, with no significant positive spillover effects of ecological functions from forest into agricultural land (Habel & Ulrich, 2020).

Decomposition requires decomposers (Hättenschwiler et al., 2005), a substrate (Chomel et al., 2015), and a suitable environment (Hector et al., 2000; R. Oliveira et al., 2019). Our findings revealed that one of the key components of the decomposer community in our site, millipedes, were not found in the maize farmland (unless refugia are available), and soil bulk density did not alter across forest-maize farmland transects (Figure 5.1), which could possibly explain the absence of decomposition spillover.

The absence of millipedes anywhere in the maize farmland could explain the lack of a trend in cellulose decomposition with distance into the maize farmland, possibly indicating that (1) the millipedes are not foraging from forest to farmland and (2) farmland is not supporting millipede populations. Previous research has revealed that millipede movement varies from 19 to 123 metres each day, depending on the species (Semenyuk & Tiunov, 2019). These millipede movement estimates represent random foraging movements rather than targeted, directional foraging because they lack effective receptors for detecting food at distance (Semenyuk & Tiunov, 2019). Unlike millipedes' populations in the forest that were out of the ground during the peak of millipede abundance estimation, millipedes in open areas possibly remained in

subterranean environment as the environmental condition during the day was not favourable for them, leading to the underestimation of their density. An alternative sampling method might be needed for better estimation. A hay-bait trap, a trap made from a wire gauze and shaped as a simple pocket that is filled with hay, could offer another option for monitoring soil-dwelling millipedes; it can capture millipedes in as little as 8-10 weeks (Tuf et al., 2015). Because millipedes are not the only decomposers in this tropical forest, additional examination of the abundance of a wider range of species within the decomposer community over time may provide a more realistic understanding of the decomposition contribution of forest fragments to surrounding agriculture.

Organic materials such as leaf litter or corn stalk litter could provide a habitat as well as substrate for millipedes in the agricultural land, which could potentially mediate decomposers, millipedes in this case, spillover (personal observation). Chomel et al. (2015) explained that litter dispersal from one habitat type to another heterogenized litter cover, allowing decomposer communities to adapt into mixed litter sources. In a more artificial manner, soil mulching by spreading organic matter (e.g., millipedes faecal pellets, maize litter, and wild shrub litter) on the ground under the crops could potentially provide habitat and refuge for the soil invertebrates to forage across habitats (Ngosong et al., 2019). However, litterfall from forests might not be sufficiently dispersed to the agricultural land, while farmers often remove or burn organic matter, limiting decomposer dispersal.

Another possibility is that maize farmlands are not supporting millipede populations. Because open canopy in the farmland allows sunlight to expose the ground and invertebrate decomposers, including millipedes, may have a limited habitat range and tolerance to changes, it is difficult for them to spread from the forest to farmland with contrasting microclimatic conditions. Because forest arthropods are often adapted to the specific environmental conditions of forests, they may avoid forest edges (Habel & Ulrich, 2020). Furthermore, the supply of cellulose or wood in the maize farming site was limited, resulting in a lack of decomposition substrate for decomposers.

However, because we did not use forest litter in the experiment, the use of cellulose bait may not accurately depict litter decomposition. To measure the decomposition of organic matter across distance relative to the forest edge, we employed toilet rolls as cellulose baits. This method has been used to analyse termite decomposition activity (Leitner et al., 2018), and we discovered that it is applicable for millipede-mediated decomposition assessment because we found limited evidence of termites consuming toilet roll at our study site (JH, personal observation). Furthermore, we use toilet roll for practical reasons because using cellulose baits

or leaf litter to evaluate decomposition in different habitats yields similar results, with decomposition being higher in forest environments than in modified habitat types (Holle & Lewis, 2022 (Chapter 2)).

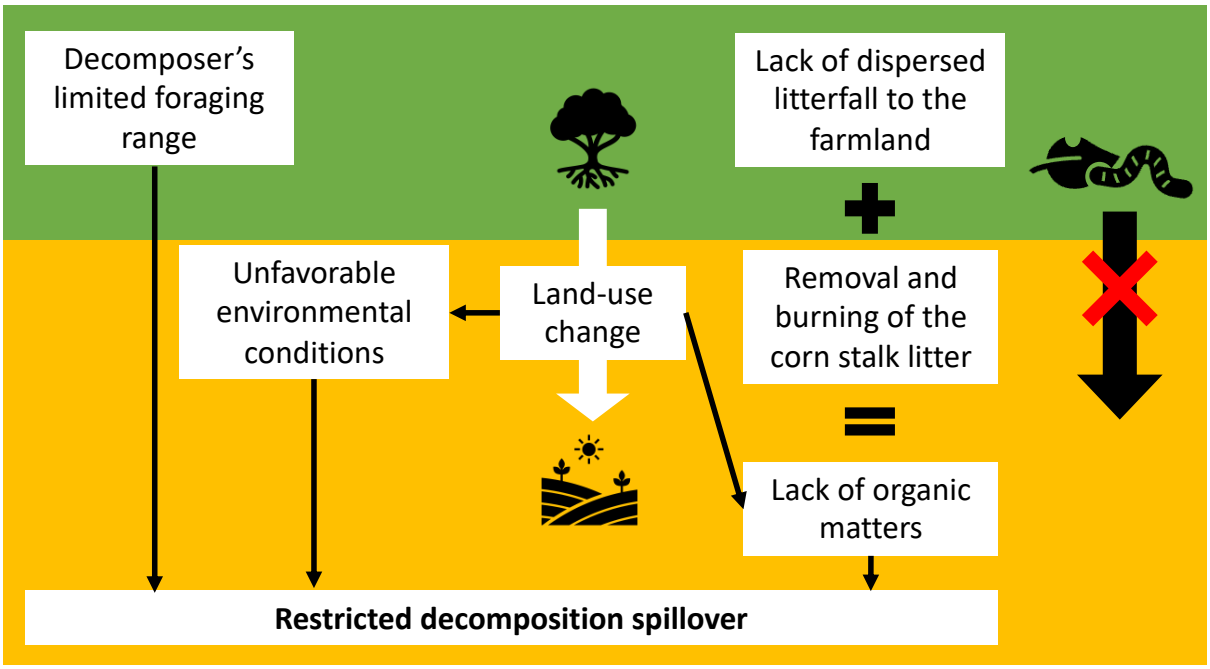


Figure 5.2. Visual explanation of the mechanisms that could prevent invertebrate decomposers from spilling-over from forests (green) to maize farmland (gold).

Unlike Gray et al. (2016), who found no pest control service spillover from riparian forest buffer to oil palm plantation, we found that tropical forest fragments contributed to predation of model pest insects in maize farmland (as also discussed in Chapter 3). Gray et al. (2016) conducted their study in 49 m width on one side of an average riparian forest buffer strip (standard deviation=30m), whereas our study was conducted in continuous tropical forest. Similarly, predation of caterpillars did not spillover from forest fragments to maize fields in central Argentina (Ferrante et al., 2017). Therefore, it is possible that a forest size determines the capacity of spillover of predation of caterpillars from forest to the agricultural land. Reduced predation of caterpillars in the smaller forest fragment corresponds with the trophic concept of island biogeography, which forecasts that predators (and parasites) will decline the most in smaller habitat patches (Anderson et al., 2019).

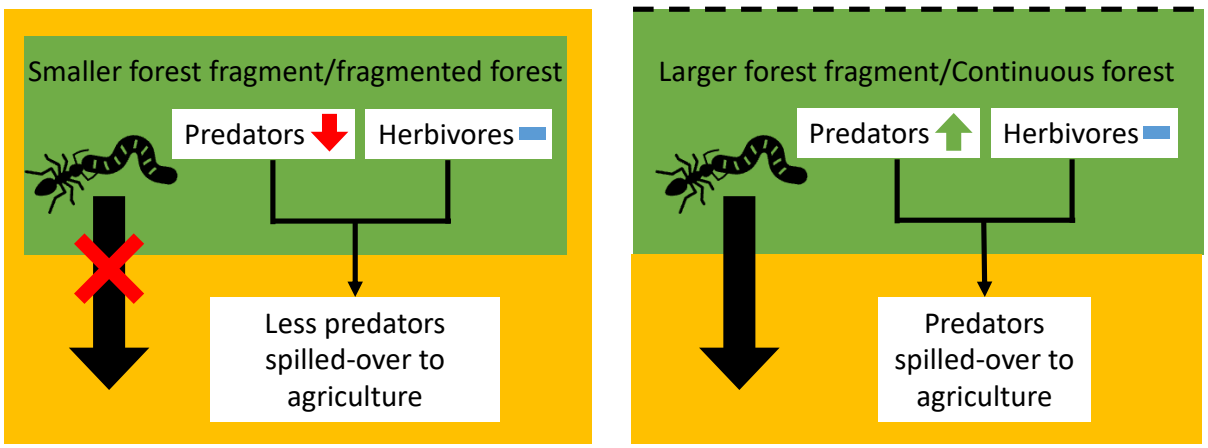


Figure 5.3. Visual explanation of the comparison of spillover of predation of caterpillars from forests (green) to maize farmland (gold) provisioned by the smaller/fragmented forest (left) and larger/continuous forests (right).

Habitat fragmentation can both increase the likelihood of species extinction and cause population outbreaks in response to a loss of natural enemies (Cobbold et al., 2005). In other words, we could also assume that fragmentation potentially reduce predator-herbivore (predation) interaction and increase herbivore-plant (herbivory) interaction. Herbivory by insect is critical not only for crop production in agricultural land (W. E. Snyder, 2019), but can also contribute to structuring and maintaining tree diversity in tropical forests (Bagchi et al., 2014; Downey et al., 2018), particularly at the early seedling stage when insect herbivory is stronger (Eichhorn et al., 2010; Vasconcelos & Cherrett, 1997). However, if we incorporate the effects of the habitat fragmentation, forest patch size solely did not seem to affect herbivory as it is a complex process that involves interactions among a range of drivers (Maguire et al., 2016). Similarly, fragmentation did not reduce herbivore growth performance (Anderson et al., 2019). Therefore, it is possible that restricted predation of caterpillars in a fragmented forest is mostly caused by the reduced predator population instead of by the increasing herbivores. This highlights the need to keep tropical forest unfragmented to provide better ecosystem functions.

Different ecosystem functions are likely to vary in the degree to which they spillover to non-natural habitats, linked in part to the habitat fidelity of the species mediating the different functions. Species associated with natural habitat (stenotopic species), those within farmland (cultural species), and those showing no preference for either habitat (ubiquitous species) are transferred from natural habitat to the agricultural land through different pathways (van Schalkwyk et al., 2020). It is possible that decomposer communities, which rely on soil quality that differs markedly between habitat types (Delelegn et al., 2017), consist of stenotopic species that were influenced by changes in environmental variables (van Schalkwyk et al., 2020). Meanwhile, caterpillar predators, on the other hand, are likely to be more ubiquitous.

Caterpillar predators might have greater mobility because they not only crawl on the ground and climb up to the leaves, but some may have flight capacity, allowing them to move freely across habitat boundaries.

Conclusion

To sum up, our study confirms that ecosystem functions can spillover from forest to nearby agricultural land, but patterns differ for different ecosystem functions. Specifically, while decomposition spilled over, predation of caterpillars did not. Of course, pest control and soil fertility maintenance are not the only ecosystem services relevant to forest regeneration and crop production; further studies on a broader range of ecosystem functions could contribute to a better understanding of how to manage human-modified landscapes more sustainably.

Chapter 6: General Discussion

Agriculture is as a major cause of deforestation, particularly in tropical regions. Managing food production while minimising environmental damage is one of humanity's greatest challenges. This thesis reports both fundamental and practical ecology research at the nexus of community ecology, agroecology, and environmental change ecology. In this final chapter, I present (1) a synthesis of the chapters of the thesis, (2) the implications of the study, and (3) lessons learned.

Summary and synthesis of the thesis chapters

In this section, I would like to synthesise the findings from each chapter into three broad streams. In the study site, despite being situated within protected areas, human activities occur and some parts of the forests, especially around the nature reserve borders, have been converted into agroecosystem landscapes that consist of three land-uses: forested areas, maize farms, and shrubland. To begin with, I evaluated the effects of habitat change on ecosystem functions (Chapters 2 and 3). Given that millipede-mediated ecosystem functions are understudied in the tropical context and that millipedes are quantitatively abundant at the study site, I took advantage of this opportunity to focus on the ecological interactions between millipedes and other litter invertebrates. Therefore, I examined the role of the invertebrate community in maintaining an important ecosystem function in a changing environment (Chapter 4). Lastly, after finding that ecosystem functions differed across habitat types, I explored potential practical solutions by quantifying the contribution of nearby forest, a habitat with the highest decomposition and predation of caterpillars values, to the less natural habitat of maize farm (Chapters 3 and 5). Understanding forest functional contributions might provide supporting evidence for how tropical forest benefits agriculture. In conjunction with additional data from the maize planting experiment, an assessment to compare crop yield produced by business-as-usual and potentially more sustainable practices (Appendix fig a.5), I am able to propose nature-based alternatives that could contribute to maintaining agricultural production while preserving natural habitats.

Impacts: Did habitat modification alter ecosystem functions?

The impacts of habitat modifications on ecosystem functions are heterogenous and idiosyncratic, depending on various factors such as (1) the intensity of the human pressures and (2) type of ecosystem. First, anthropogenic disturbances that do not drastically modify the forest structure such as selective logging of forest might cause less alteration of ecosystem functions (Ewers et al., 2015). However, the intensity of the habitat modification in the study

area is high, indicated by the completely modified physical structures of the maize farmland and shrubland habitats. Unlike the impact of forest logging, clear-cutting tropical forests into bare land followed by establishment of agriculture could potentially eliminate ecosystem functions (Chapters 2 and 3), simplify the habitat structure and biodiversity as well as change the microclimate (Appendix fig a.1). As a result, some of the species occupying the functional niches, in this case is decomposers, are possibly missing and not substitutable by other species. There is a possibility that the gradient of human disturbance intensity shows a similar trend to the that for ecosystem functions. In this thesis, I assume that shrubland is a transition between forest (natural habitat) and farmland (human-modified habitat), as shrubland is potentially a part of the succession processes after a strong disturbance (Rubiano et al., 2017). Moreover, we observed the gradient of the ecosystem functions that are well aligned to the gradient of the habitat modification where ecosystem functions in the natural habitats tend to be higher than that in the human-modified habitats (Chapters 2 and 3).

Secondly, different ecosystem types might have specific responses to similar drivers of habitat modification. Tropical forest ecosystems which are situated at lower latitude with more complicated ecological interactions (Schemske et al., 2009) and higher terrestrial species diversity (Brandon, 2014) might have higher resilience towards disturbance than, for example, grasslands with fewer species. In more diverse ecosystems, multiple species often occupy similar ecological niches, providing ecological redundancy: the roles of some species that are affected by a disturbance might be substituted by other more disturbance-tolerant species with otherwise similar niches and functions. This ecological redundancy potentially positively affects community stability and resilience to disturbance (Biggs et al., 2020). In addition, the extent of the ecological redundancy shifts as species role's change in different environmental conditions (Fetzer et al., 2015). Problems arise when habitat modification directly eliminates the only one or few species occupying an ecological niche with unique roles or indirectly increases the competition among these species. In this case, there would be a missing ecological role in the ecosystem that leave ecological niche unfilled (Ashby et al., 2017), making the effects of habitat modification on ecosystem functions more significant.

Numerous studies have explored the impacts of habitat modifications, especially by agricultural activities, on ecosystem functions (Howe et al., 2009; Nurdiansyah et al., 2016; Denan et al., 2020). However, little is known about how small-scale, non-indutrialised agriculture affects ecosystem functions. Given that small farms tend to have higher yield and biodiversity (Ricciardi et al., 2021), the small size and often low-intensity farming practices of small-holder farms often lead researchers to assume that they have low ecological impacts. In

this study, I found that even small-holder farming can detrimentally alter decomposition of organic matter and predation of caterpillars (Chapters 2 and 3). Either small-scale or industrial agriculture are likely to have pronounce negative impacts on ecosystem functions when they radically modify habitat structures.

Mechanisms: How does a changing environment affect ecosystem functions mediated by the invertebrate community?

In this thesis, I experimentally explored the impacts of two drivers of environmental change: land-use change due to agricultural activities (Chapter 2, 3, and 5) and climate change in the form of extreme precipitation change (Chapter 4). Different drivers of environmental change have different impacts on the ecosystem functions that are provisioned by the invertebrate community. For example, agricultural management and climate change not only alter microclimate, but also modifies soil structure and soil chemistry. I investigated the impacts of land-use change on both decomposition and predation of caterpillars, but the impact of precipitation change was only investigated for decomposition. I suggest that land-use change alters ecosystem functions by modifying the invertebrate community structure (direct) and by modifying invertebrates' habitat structure (indirect).

While measuring a wider range of invertebrate-mediated ecosystem functions, such as pollination, dung removal, and seed dispersal, would give a better picture on how tropical agroecosystem functions operate, I chose to focus on invertebrate decomposer communities and arthropod predators as these two are the ecosystem function most s relevant to potential crop failure at the research site (Personal observation). A priority for future work would be to assess other parameters related to these ecosystem functions. For example, other aspects related to predation of caterpillars such as quantification of herbivory damage and predator biodiversity might allow a better understanding of patterns and mechanisms of predation of caterpillars along the gradient of habitat modification. Moreover, the effects of the land-use change on each of the invertebrate groups that provide ecosystem functions are expected to be idiosyncratic, thus the discussion will explain these separately for invertebrate decomposer communities and arthropod predators.

- *Effects of land-use change on invertebrate decomposers*

In this study, although decomposition is mediated by various biological components, such as microorganism, fungi, and macrofauna, I particularly focus on the impacts of environmental change on the invertebrate decomposer community. In general, land-use change due to agriculture has been proven to decline invertebrate biomass and abundance. Previous

study showed that tropical primary forest conversion into oil palm plantation reduced invertebrates in all compartments of the ecosystems, such as epiphytic bird's nest ferns, the canopy, and leaf litter (Turner & Foster, 2009). Invertebrate decomposers are often used as a bioindicator of the changing environment. For example, millipedes are used as bioindicators because they have narrow tolerances and consequently respond rapidly to environmental change (Masse et al., 2017). In addition, both land-use and climate change affect invertebrate decomposers' habitat structure. This changing environment alters microclimatic conditions, potentially making them less favourable for decomposition. The data of the decomposer invertebrate community across habitat types and post-mesocosm invertebrate community composition is available on the Appendix fig. a.2. and fig a.3.

Decomposition is promoted by higher humidity and temperature (Dan et al., 2016; Salinas et al., 2011) and a nutrient-rich environment (particularly for fungus-mediated decomposition) (Pascoal & Cassio, 2004), which are generally influenced by the changing environment. For example, logging, which often takes place for agricultural land preparation, impacts tropical forest ecosystems in various ways, especially by altering the microclimate, such as temperature, air moisture, and light penetration to the forest (de Frenne et al., 2021). Tropical forest conversion into plantation not only affects microclimate, but is also expected to alter nutrient cycle through reduced litterfall (Zhu et al., 2022). Similarly, in arid regions, soil nutrient availability and soil water content could be reduced under changing land-use (R. Zhang et al., 2020).

Given that this study focuses on land-use change due to agricultural activity, there are some effects of the farming management treatment (i.e. tillage, fertilizer, and pesticide) that are important to note. Although fungicide apparently did not significantly affect decomposition and the invertebrate decomposer community (Chapter 3), there is a possibility that higher intensities of fungicide treatment and other farming practices, such as soil tillage and application of fertilizer and herbicide, would have effects on both invertebrate and microbial decomposers. In an Australian vineyard, soil tillage affects the invertebrate composition and potentially negatively affects the abundance of beneficial invertebrate groups (Sharley et al., 2008). Similarly, all types of pesticides tested negatively affected soil invertebrates in a study that. (Gunstone et al., 2021). Therefore, I suggest that conventional small-scale agricultural management might pose a negative impact on the invertebrate decomposers thus reducing decomposition capacity.

- *Effects of land-use change on arthropod predators*

As the most dominant potential predators are ants (Hymenoptera: Formicidae), I focus on the impact of the changing environment on ant communities. Ants' responses to the changing of the abiotic factors associated with climate change are not fully clear (Parr & Bishop, 2022). Unlike the decomposition provided by the invertebrate decomposers, predation of caterpillars by ants is transferred from the forested habitat to the open-canopy habitat of the maize farmland (Chapter 5). This might indicate that changing habitat structure has less impact on the ant community than on the invertebrate decomposer community. Some ant species may benefit from higher habitat openness in the maize farmland. Habitat openness is one of the main drivers of variation in the ant communities, which is proven to increase nest establishment and to improve colony productivity (Andersen, 2019). A study in the Sumatran rainforest showed that forest conversion to monoculture plantation favoured generalist ants with large colonies (Kreider et al., 2021).

However, ant communities might be negatively affected by land-use and climate change. Some ant species nest and forage in the forest canopy. Forest canopy removal seems to have a substantial impact as it could eliminate the entire nests of these ant species. In addition, being ectothermic organisms, ant communities might become less stable under warming condition (Diamond et al., 2016). In wet tropical environments, drought may reduce ant richness and alter species composition (Almeida et al., 2020). In the Mexican tropical dry forest, human disturbance homogenises resource availability and thus the ant community is also homogenised (Hernández-Flores et al., 2021).

- *Potential ecological value of the shrubland*

Given that *C. odorata*, an invasive alien plant species, is a dominant species in the shrubland sites, it is commonly perceived that the negative effects of *C. odorata* dominated shrubland outweigh its benefits. In addition, the shrubland is not producing any yield so that it is considered as a non-productive land. However, despite the contrast different is extensively compared between ecosystem functions measured in the forest and corn farmland, it is noticeable that shrubland appears as a transitional habitat. Leaf litter decomposition rate in the shrubland was between those in the forest and farmland (Chapter 2). In the study sites, farmers often abandoned agricultural land in non-planting season, leaving shrubs, including *C. odorata*, grow naturally in the land. In the planting season, mostly during rainy season, farmers clear the shrubland and revert it into agricultural land. This practice in integrating *C. odorata* fallow in a cropping system might benefit sustainable food production in the buffer zone of a Nature

Reserve in the Ivory Coast as well as reduce pressure on forest islands (Tondoh et al., 2013), mainly by improving soil biology and nutrient availability (Koné et al., 2012).

I am not aware of any study on how *C. odorata* dominated shrubland contributes in pest-control, however, some shrubland sites seem to have higher caterpillar predation than forests (Chapter 3, fig 3.2), indicating that shrubland could potentially host the predators of the caterpillar, which fall into arthropod group, particularly ants. Some ant species may be favoured by less shaded environment in the shrubland as habitat openness is one of the main drivers of variation in the ant communities, where more open habitat is proven to support nest establishment and to improve colony productivity (Andersen, 2019). Therefore, management of the shrubland needs to be taken into account in the tropical agroecosystem landscape.

Solution: Do natural habitats provide ecosystem functions to modified agricultural habitats?

Tropical forests often harbour higher biodiversity and more complex and stronger ecosystem functions than modified habitats (Lewis, 2009). Previous studies have reported that natural habitats can 'spillover' components of the invertebrate community to nearby non-natural habitats (Lucey & Hill, 2012). However, we found that natural habitats might provide some ecosystem functions but not others. Specifically, decomposition was not transferred from forest sites to nearby maize farmland, while spillover of predation of caterpillars was observed (Chapter 3 and 4).

Ecosystem function provision by tropical forests might differ temporally. The study was conducted in the rainy season as maize was exclusively grown in this season, which is considered as a peak time for ecosystem function spillover. If crops were planted all year around, the annual dynamics of the ecosystem function spillover might be observable. The contrast in microclimatic conditions between the forest and maize is most marked during the dry season, making the maize an even less favourable environment for forest decomposers.
Given that temperature is the most important environmental factor affecting insect population dynamics, warming, which often occurs in the dry season, might expand the habitat range and increase the reproduction rate of agricultural pests (Skendžić et al., 2021). In this case, invertebrate predators are expected to provide less pest control service in the dry season, when their resources (pests), exceeds the capacity of the predators to predate pests. Thus, crops might be more severely affected by the herbivorous insects in the dry season and in a long-term climate warming.

Ecosystem function spillover is probably site-specific. We noticed contrasting findings between the two existing studies of spillover of predation of caterpillars in forest-maize

farmland systems, which were carried out in different landscapes. While we found a significant spillover effects, Ferrante et al., (2017) did not record a significant change in predation with proximity to forest fragments. In terms of the potential caterpillar predators, we found that arthropods are most likely to be the dominant predators, while Ferrante et al., (2017) record a much higher incidence of vertebrate attack in their study. These differences might in part reflect genuine differences in predator identity, activity and impact between the two specific landscapes. I suggest that replicating the studies in the other forest-maize farmland systems might provide a clearer understanding of the factor influencing measures of predation spillover. Global study of the predation of herbivorous insects using plasticine caterpillars showed that latitude and altitude influence predation of caterpillars (Roslin et al., 2017). Therefore, it is possible that the combination of latitude and altitude could result in the observable pattern of the spillover of predation of caterpillars to agricultural land.

Although studies on edge effects on species richness and abundance are widely investigated, the responses of the ecosystem processes to the edge effects, particularly those related to the tropical forest invertebrates, has been essentially overlooked due to logistical and taxonomic constraints (Foggo et al., 2001; Riutta et al., 2016). This thesis shows that there is no significant different of the decomposition and caterpillar predation in the forest edge (Chapter 5), probably due to the short interval between data points in the forested areas. However, studies covering wider data points from forest edge to the interior demonstrate that soil fauna feeding activity and wood decay was lower by 40% and nearly 15% respectively at the temperate forest edge than in the interior (Crockatt & Bebber, 2015; Riutta et al., 2016). On the other hand, how edge effects influence caterpillar predation has been inconsistent. Caterpillar predation by insectivorous bird is peaked in the temperate forest edge (Barbaro et al., 2014; Bereczki et al., 2015; González-Gómez et al., 2006), meaning that there is a positive edge effect on avian insectivory. Meanwhile, a study conducted in the tropical region showed no edge effects on caterpillar predation rate by insectivorous birds (Koh & Menge, 2006). It is unclear whether the edge effects on the predation rate is driven by the latitudinal variation or not. Edge effects might also vary under seasonal differences. For example, predator spillover from natural habitats into nearby farmland can occur during the early stages of crop growth, but be reversed later in the season or in the post-harvesting period (Rand et al., 2006). As a consequence, this direction shifting of the predator spillover will increase the predation rate in the forest edge (positive edge effects). Therefore, different ecosystem functions have idiosyncratic responses that require an understanding of the local and temporal contexts.

Practical implications in conservation

Given that agriculture is the major driver of deforestation in tropical region, and also contributes to climate change, I believe that this thesis has further implications in the supporting invertebrate conservation and sustaining tropical agriculture. Here, I would like to discuss about invertebrate conservation and sustainability in agroecosystem.

Invertebrate conservation

Although invertebrates are a dominant component of biodiversity globally, particularly in tropical regions (Ewers et al., 2015), invertebrate conservation receives little attention (Eisenhauer et al., 2019). Having important roles in maintaining ecosystem functions does not necessarily engage the public to conserve them. Instead, while providing ecosystem services, invertebrates are often associated with their disservices such as acting as pests and spreading disease (Eisenhauer & Hines, 2021), leading to negative public perceptions towards invertebrates (Leandro & Jay-Robert, 2019). In our study site, farmers burned plant litter, including millipedes that took a refugia under the plant litter (fig. 6.1.), indicating that their presence and their ecological roles are not well understood and utilised by the farmers.



Figure 6. 1. Millipede carcasses visible in the post litter burning by farmers.

Despite having a high abundance and a potential role in maintaining decomposition process under changing precipitation conditions, the millipede species (*Salpidobolus* sp.) in our study site is likely to be an undescribed species, indicated by (1) no species with the distinctive morphological characteristics of this species that have been discovered in Sulawesi region and (2) DNA sequencing showed that there is no millipede species that has more than 75% similarity to the *Salpidobolus* sp. in the study sites (Unpublished data). Protecting and studying undescribed species is difficult. Therefore, further attempt to describe and compare these millipedes with existing described species might have a positive consequence for

invertebrate conservation. This problem arises not only for this particular millipede species but also other invertebrate species in Sulawesi. Invertebrate surveys and identification are needed to provide baseline biodiversity data for the region. Meanwhile, invertebrate conservation at the habitat level is relevant to the sustainability of agroecosystems, as explained in the following section.

Sustainable agriculture

Given that some invertebrates exclusively inhabit natural habitats and invertebrate-mediated ecosystem functions in agroecosystems could be either independent or dependent on forests, invertebrate conservation should be ideally conducted at the landscape level, that consists of both natural and human-modified habitats (mainly agricultural land). Here, I would like to provide an idea on how to conserve forest while supporting sustainable crop production.

Conservation of agroecosystem landscape can adapt the conservation hierarchy framework, a commonly used tool to guide efficient conservation actions, that consists of (1) avoid, (2) minimise, (3) remediate, and (4) offset (Arlidge et al., 2018). In the tropics, increasing food production is often associated with increasing the area of agricultural land by sacrificing forest cover. To minimise the impacts of the agriculture on the environment, there are two strategies, land-sharing and land-sparing, that are controversial and often debated (Loconto et al., 2020). Land-sharing is a concept where agricultural land should be managed sustainably and in a wildlife-friendly way, while land-sparing strategies set aside high-yielding agricultural area and natural habitats. My thesis work provides some evidence that forests potentially contribute to food production, particularly in supporting an argument that land-sharing and land-sparing are not mutually exclusive; both are required to balance management needs for agroecosystem multifunctionality (Grass et al., 2019). Therefore, I would suggest a concept that combines the outcomes of this study and previous frameworks, conservation hierarchy framework and land-sharing/land-sparing strategies.

Ideally, as much as possible coverage of the natural habitat should be protected; one way to do so is via legal protected status (Jepson et al., 2017), corresponding to “avoidance” in the mitigation hierarchy concept and land-sparing strategy (fig. 6.2.). However, many pristine forests are not legally granted for that status. In addition, forests are vulnerable to agricultural expansion even if they have protected status (Reyes et al., 2010). In the study site, deforestation, mainly driven by agriculture, is observed within the nature reserve borders. Along with forests, maize farmland and shrubland sites in Chapters 2 and 3 are administratively situated within protected areas. The trend of agriculture expansion within the protected areas has been

occurring for decades where the degraded condition of the forests often becomes the driver in lowering the protected status of the areas. Major land-use change started in 1978-1996 when the government had promoted a transmigration programme where people from Java, the main island of Indonesia, were relocated to rural areas, including Gorontalo province, to establish new settlements with new agricultural land. As transmigrated people might not inherit traditional ecological knowledge (TEK) of the customary communities, their farming practices and natural resource management were often not ecologically friendly. Over the past four decades (1978-2018), the forest cover of Panua Nature Reserve has decreased by 6,482 hectares, approximately 13.2% of the total area (Appendix Paper a.1.).

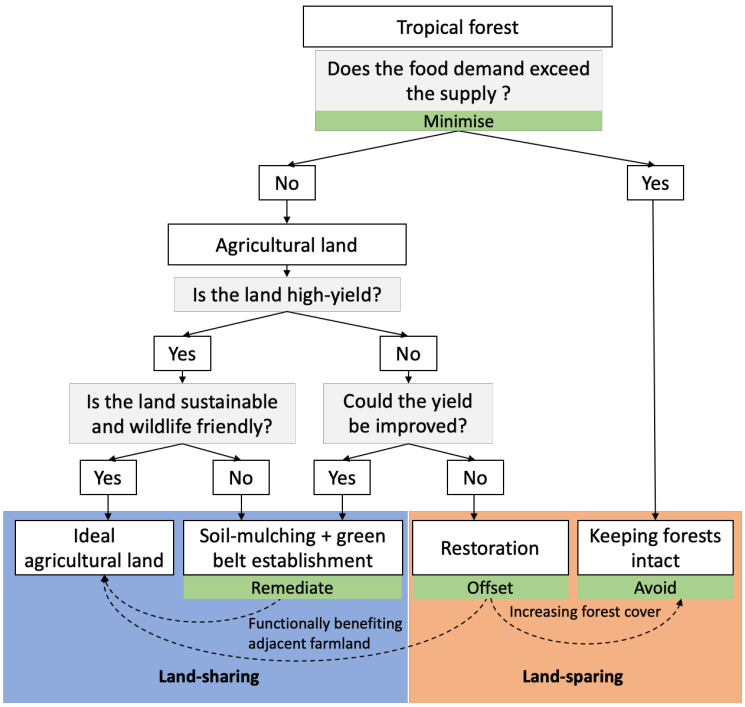


Figure 6.2. A schematic concept for sustaining agroecosystems that combines the mitigation hierarchy framework (highlighted in the light green shading), and land-sharing/land-sparing strategies.

When land-use change is inevitable, minimising the impacts of agriculture on the invertebrate communities would be the next step. At the same time, addressing two of the major agricultural issues that might cause crop failures, soil infertility and pest attack, is necessary. To prevent this, conventional agriculture management practice uses extensive chemical fertilizers and pesticides, which negatively affect the environment. The outcome of this study (Chapter 5 and Appendix fig a.4.) provides some evidence to minimise the agricultural impacts while addressing abovementioned agricultural issues.

Because decomposer invertebrate communities do not seem to be transferred from forest to maize farmland (Chapter 5), probably because agricultural land does not provide favourable microclimate for decomposer invertebrates, I suggest that soil mulching by

spreading organic matter (i.e. millipedes faecal pellets, maize litter, and wild shrub litter) on the ground under the crops could potentially provide habitat and refuge for the soil invertebrates to forage across habitats (Ngosong et al., 2019; fig. 6.3.). This would not only provide habitat for soil invertebrates, but it could also naturally fertilize soil, substituting the use of fertilizer while producing similar crop yields to business-as-usual agriculture (i.e. application of fertilizer and pesticide) (Appendix fig a.4.). This idea is supported by a previous study in the tropical agriculture of the Southwestern Colombia where green fertilizer applications can improve the soil's ecological state (Urbano et al., 2019).



Figure 6.3. Millipedes taking refuge under plant litter in the maize plants that produced equal yield to the fertilizer treated maize plants.

Meanwhile, conventional agriculture management practices make extensive use of pesticides to reduce pest attack. I suggest that this could potentially be substituted by biological control provisioned by arthropod predators in natural habitat. Chapters 3 and 5 show that predation of caterpillars is a forest-dependent ecosystem function where it is spilled-over from forested areas to the maize farmland.

Improving the capacity of the herbivorous insect predation could be done by creating habitats for them in the agricultural landscape. For example, restoring "green strips" across agricultural land could increase the farm's exposure to surrounding natural ecosystems, hence providing habitats for insect predator groups and enhancing pest management in maize farming (fig. 6.4.). Although a study in southern Costa Rica found that forest restoration strategies were not proven to result in a similar litter arthropod community to natural forests after 8 years of recovery (Cole et al., 2016), I found that 14 years of natural regeneration restored

decomposition rates as well as spillover of predation of caterpillars (Appendix fig a.5.; a.6.; a.10). In addition, the presence of the vegetation could potentially help reducing the likelihood of soil erosion, especially for farmland on steeper slopes that is commonly found in the study site (personal observation). Forest restoration, either in the degraded parts of the protected areas or outside of the areas for offsetting the deforestation, is expected to conserve invertebrates. Moreover, halting forest degradation through forest restoration has been one of the challenges in plant ecology (Yannelli et al., 2022), especially since the UN has announced 2021-2030 as the Decade on Ecosystem Restoration (https://undocs.org/A/RES/73/284).

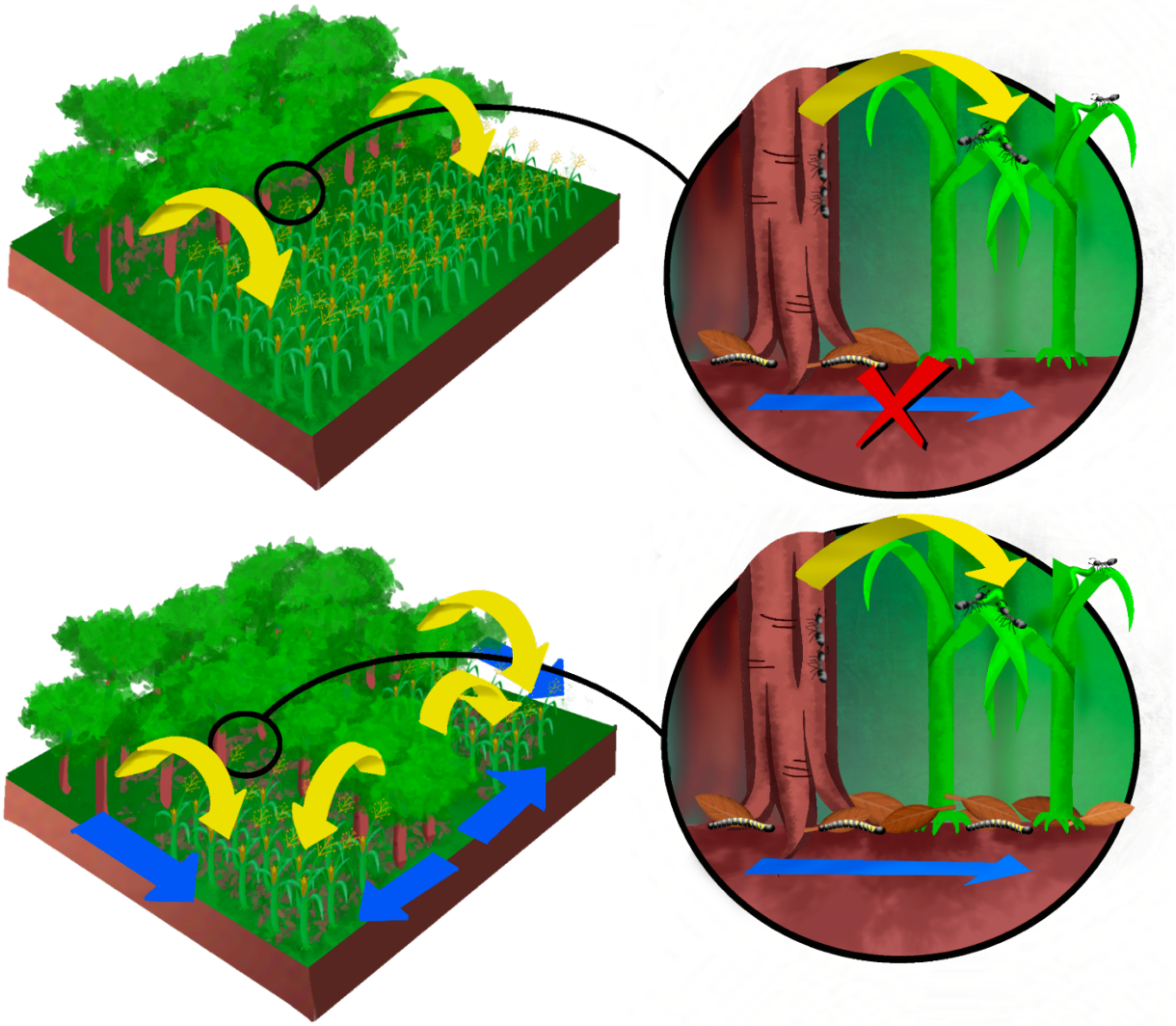


Figure 6.4. Visual representation of the expected effects of the forest strip establishment in agricultural land and soil mulching in agriculture. Top: current farming practice; bottom: farming practice involves forest strip establishment and soil mulching. Yellow arrows: Caterpillar predation spillover; Blue arrows: expected decomposer spillover.

Lessons learned: DPhil as an academic life journey

In the last part of the General Discussion section, I would like to reflect on three lessons I learned when I conducted this thesis project. First, I figured out that ecological research can be done with a simple yet robust methods. By having an appropriate experimental design, I have conducted several experiments with a relatively simple instruments and affordable materials. This is particularly important for ecological researchers in developing countries where research facilities and instruments are limited. Having a skill in performing a low-cost but reliable research methods will keep myself productive under a resource-limited setting.

Secondly, conducting field ecological research can be challenging, especially because of the uncertain conditions, including most recently the global pandemic that been limiting the ability of researchers to reach their research sites. This is crucial for researchers who are conducting research overseas as international travel was severely disrupted. Uncertainties often happen in the field where uncontrolled factors play a role. For example, I was unexpectedly unable to collect some samples at the planned time due to rain that was flooding the access to the study site, thus sample collection had to be postponed. On another occasion, one of the shrubland study sites had been clear-cut, including removing all the samples and instruments set around that area. These uncertain events have forced me to react quickly to properly troubleshoot the non-ideal situation, such as by modifying the methods, incorporating the inconsistencies in the statistical analysis, or preparing for some extra sites during the planning and preparation processes.

Thirdly, given the nature of my project that is independent research, I realised that this thesis lacks collaborative efforts. Conducting an independent research project is clearly useful to prepare myself to become an independent researcher who is responsible for all aspects of the research project including designing the research, fund-raising, and conducting the research. However, having multiple authors to get involved will have some other benefits, such as more intense brainstorming that can lead to better written publication. In case of this thesis, most of the work from the planning to the writing process has only involved the student and one supervisor, with some comments and input from research group members and journal reviewers. Balancing the independent and collaborative works of research project could potentially maximise the outcome of the thesis.

Lastly, unlike other branches of biological science, ecological research is uniquely associated with a wide range of sciences, from natural to the social science. In particular, research in the field of the environmental change ecology needs an understanding of the

relevant environmental and socio-political issues to formulate appropriate research questions. For example, to decide which ecosystem functions to measure, I had to identify the causes of the crop failures that are experienced by the farmers. I also focused on the small-holder farming activities as small-holder farmers are more vulnerable and represent the majority of the farmer communities in tropical regions. I hope that understanding the relevant issues and social context helped me to make my thesis more impactful and meaningful.

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Study site coordinates

Table 1. Coordinate location of blocks. KN: Kebun Nurdin; CD1: Cek Dam 1; CD2: Cek Dam 2; BL: Bulangita; TE: Teratai; KB: Karya Baru.

Blocks	Coordinate
KN	0° 28’ 50.8” N, 121° 59’ 22.0” E
CD1	0° 29’ 38.9” N, 121° 59’ 57.5” E
CD2	0° 29’ 47.7” N, 121° 59’ 40.1” E
BL	0° 30’ 03.9” N, 121° 59’ 18.0” E
TE	0° 29’ 00.1” N, 121° 58’ 52.9” E
KB	0° 36’ 11.7” N, 122° 05’ 38.6” E
MIX	0° 36’ 43.6” N, 121° 05’ 47.2” E (Maize farmland) 0° 28’ 29.2” N, 121° 58’ 12.2” E (forest) 0° 29’ 00.8” N, 121° 59’ 24.5” E (shrubland)

1. Additional results

   a. Temperature and humidity across habitat types.

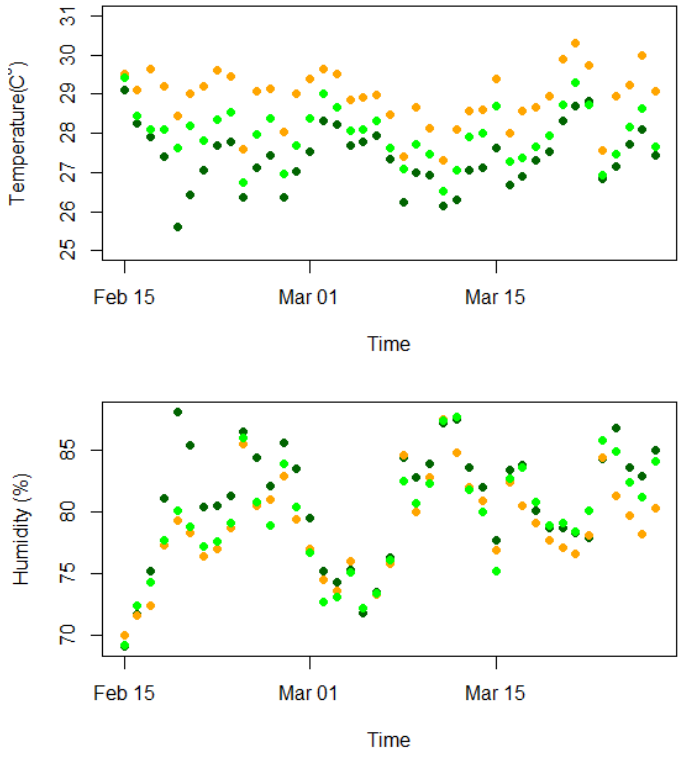


Figure a.1. Air temperature (top) and air humidity (bottom) in forest ● (n=4), shrubland ● (n=3), and Maize farming ● (n=5), recorded from 15th February to 27th March 2019. Air temperature and air humidity are significantly different in the three different habitat types. Air temperature was higher in the maize farmland and lower in the forest site. Meanwhile, humidity was higher in the forest and lower in the maize farmland.

b. Invertebrate decomposer community across habitat types.

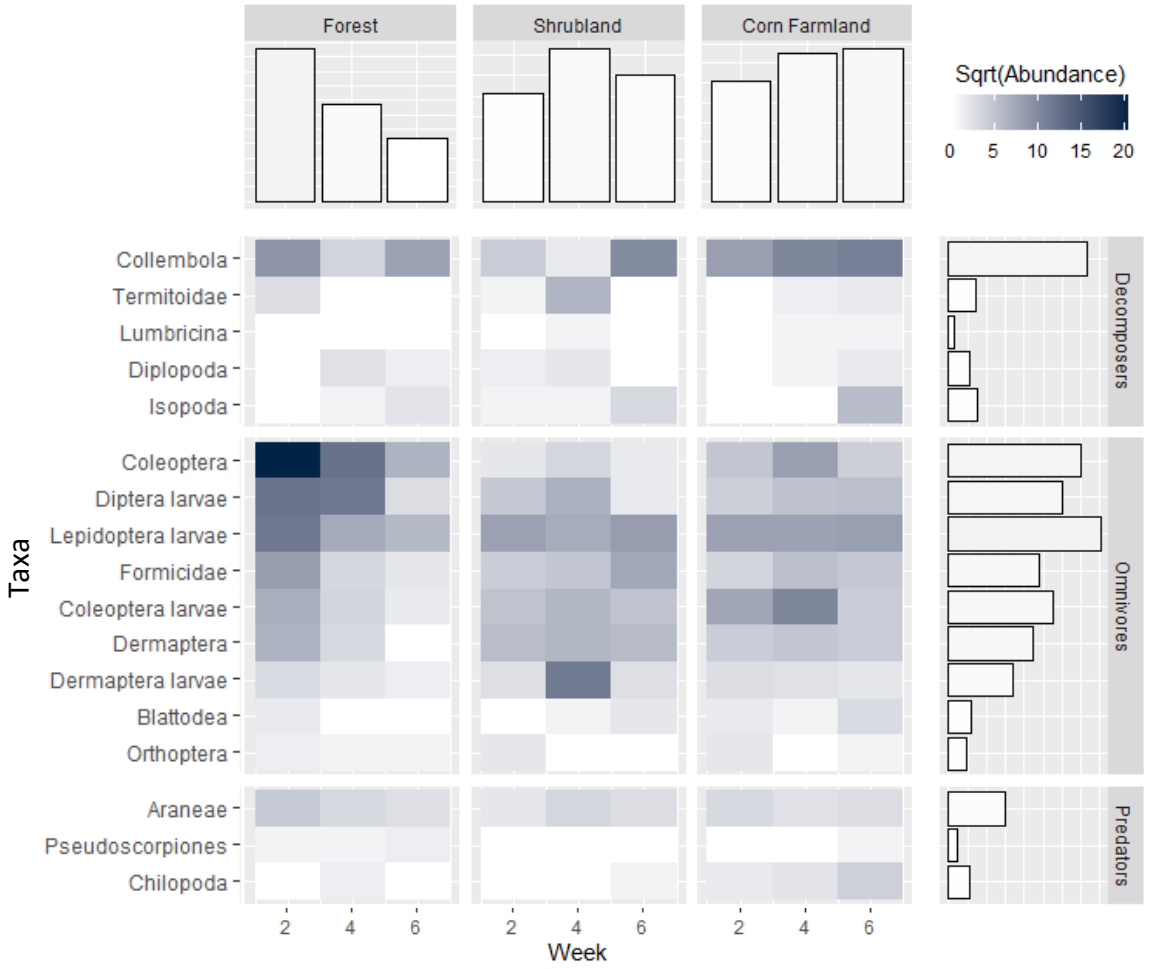


Figure a.2. Abundance of litter invertebrate in three different feeding guilds across land-uses. Taxa were sorted by abundance of litter invertebrate collected in the 2nd week in forest habitat, which was square-rooted to improve visualisation. Histograms show the mean square-rooted abundance, indicated by the bar colour, of invertebrates over time at each habitat (top) and within taxa at each of three feeding guilds (right).

We identified 3570 individual litter invertebrates in total. Their abundance differed among habitats and was highest in forest sites (1571 individuals) followed by corn farming (1093 individuals) and shrubland (906 individuals). Decomposer and predator guilds were dominated by Collembola and Araneae, respectively, in all habitats, while the dominant group were more varied within the omnivore guild. A declining abundance pattern was apparent for the omnivore community in forest habitat over time.I nvertebrate abundance in the forest site is decreasing over time, possibly due to less leaf litter substrate within litterbags which attracted less invertebrates to colonize the leaf litters. Given that decomposition in the corn farmland did not occur quickly, similar invertebrate abundance in the fourth and sixth week in the corn

farmland might indicate that the invertebrate abundance was not limited by the reduced leaf litter substrate.

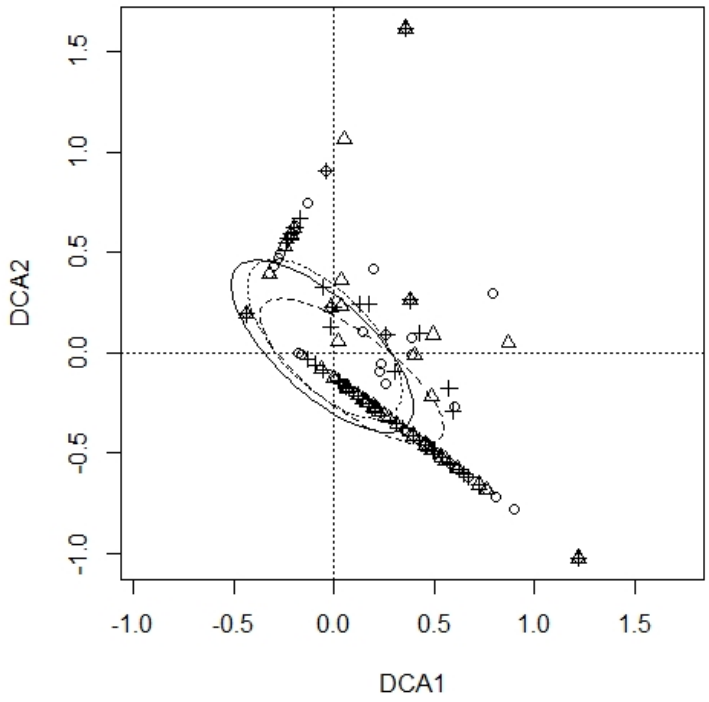


Figure a.3. Detrended Correspondence Analysis (DCA) diagram showing feeding guild scores, indicating that community composition is similar in all habitat types. Ellipses show standar deviation around the mean for each habitat types (Dotted = Forest, solid = Shrubland, dashed = Maize farmland). (circle= decomposers, triangle=omnivores, plus= predators).

c. Post-mesocosm experiment invertebrate community.

(A)

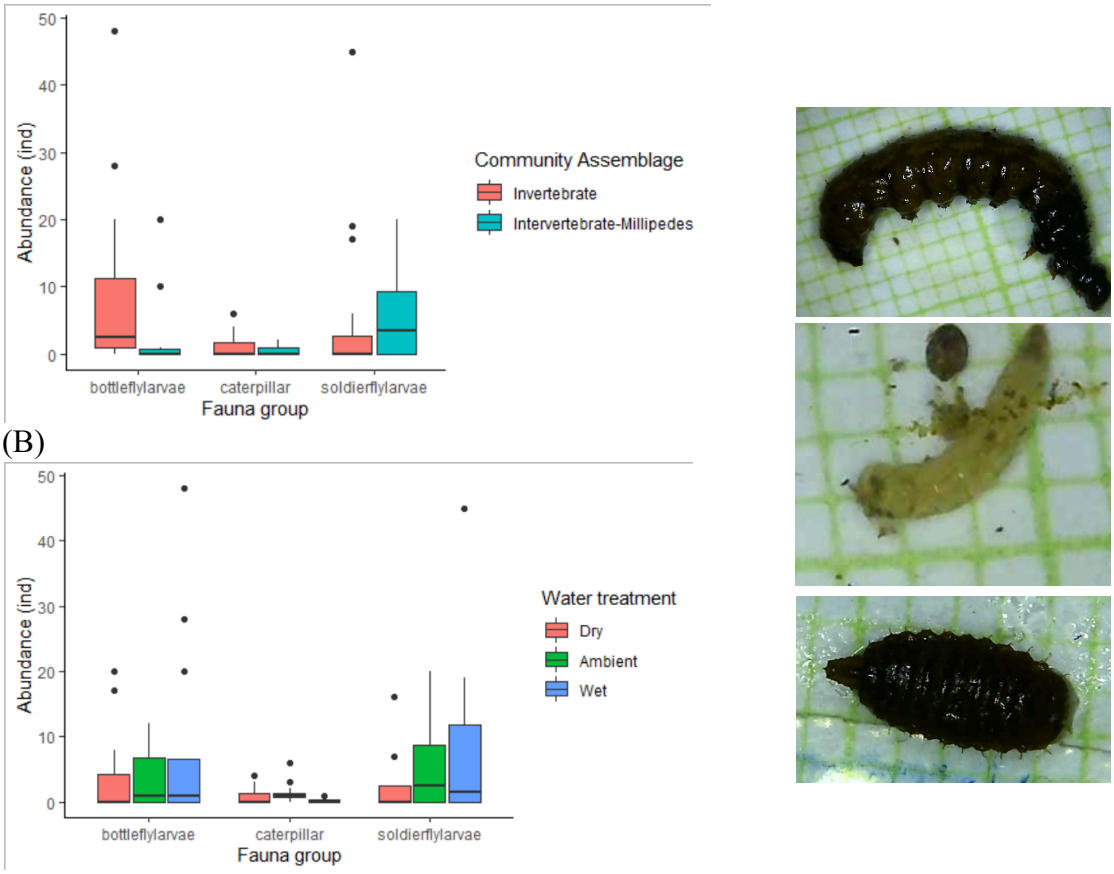


Figure a.4. The abundance of macrofauna community collected from the post-mesocosm experiment of decomposition that was mediated by various macrofauna community compositions (A) and under different moisture levels (B). Components of the boxplots are median (central bar), upper and lower quartiles, and whiskers including points within 1.5 interquartile range (n=72).

The abundance of post-experiment litter invertebrates collected after the mesocosm experiment termination is presented in the boxplot of figure a.4. As the invertebrates were hand-collected, we merely presented the abundance of macroinvertebrate individuals that are visible with naked eyes by assuming that those dominantly contribute in decomposition are rather larger sized invertebrate. We found that there are three main macroinvertebrate groups, which are bottlefly larvae (Diptera), caterpillar (Lepidoptera), and soldier fly larvae (Diptera); all are omnivores that contribute to the decomposition of leaf litter. A model that includes interactions has a lower AIC value; therefore, we proceed with this model for the data analysis of this result. Invertebrate abundance was influenced by a variety of fauna groups ($F_{2,90}$=4.978, p=0.0089), the interaction between water treatment and community assemblage, and overall

interaction among fauna groups ($F_{2,90}$=6.879, p=0.0016), water treatment and community assemblage ($F_{4,90}$=2.706, p=0.0351). Without millipede presence, Diptera larvae had a higher abundance in the wetter soil condition. Contrarily, when both litter invertebrate and millipede coexist in the mesocosm setting, Diptera larvae abundance tends to get decreased in the wetter soil condition. Among fauna groups, caterpillar (Lepidoptera) has lower abundance than bottlefly larvae and soldier fly larvae. Other independent main effects and interactions did not differ significantly.

d. Corn yield comparison between BAU and sustainably treated corn plants.

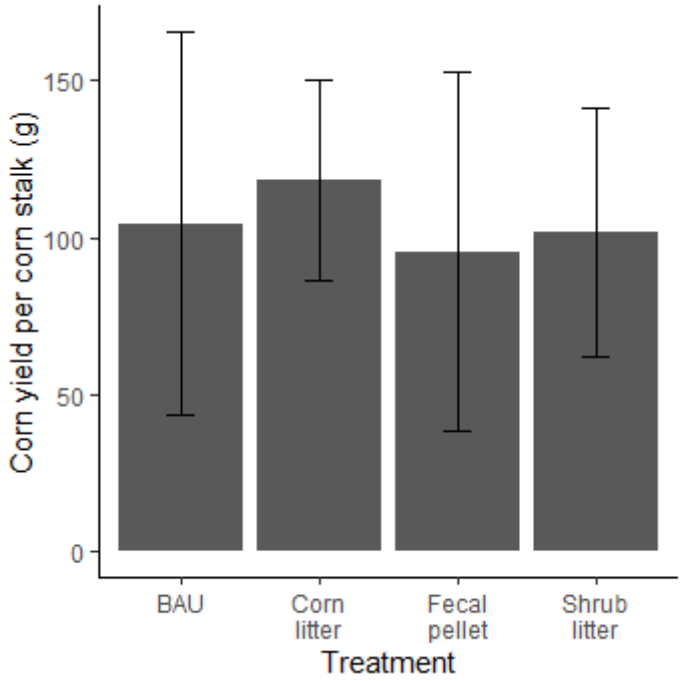


Figure a.5. Corn yield did not differ between BAU and sustainably treated corn plants.

In this mini experiment, I treated 80 individual maize plants with 4 different treatments, which are business-as-usual (BAU), mulching with corn litter, millipede fecal pellet and shrub litter. BAU treatment involved the application of the non-organic substances (fertilizers, pesticides, and herbicides). Corn litter, millipede faecal pellet, and shrub litter were not exactly quantified and were mulched in a practically manageable quantity. All maize stalks produce 2 corn cobs except 4 stalks that only produced a single cob. Crop yield is defined as the weight of the corn seeds separated from each cob without the inner cob. There is no significant different of the corn yield under different treatments.

e. Caterpillar predation spillover provided by primary and regenerated forests

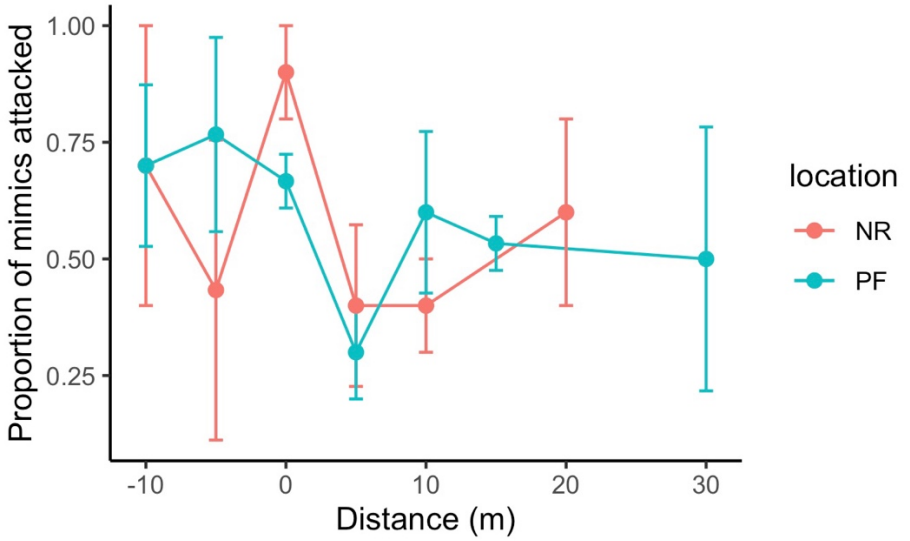


Figure a.6. Predation of caterpillar was similar between primary (PF) and naturally regenerated (NR) forests.

Six line transects were established running from the edge of the primary forest (PF) and naturally regenerated forest (NR) into the maize farmland, with sampling sites within the forest (-10 m, -5 m) at the forest edge (0 m), and in the corn farmland (5 m, 10 m, 15 m, and 30 m). Naturally regenerated forest once was a farmland that has been abandoned in 2006 so that vegetation was naturally colonizing the land for 14 years. At each sampling site, caterpillar predation was recorded by attaching plasticine caterpillars in the foliage part of the vegetation using super glue for two days. I found that there is no significant different of the proportion of attacked plasticine caterpillars between PF and NR transects.

f. Caterpillar predators (arthropods, birds, mammals, and reptiles) across habitat types



Figure a.7. Samples of attack marks on plasticine caterpillars: (top-left) Bird marks, (top-right) Arthropod attacks, (bottom-left) reptile marks, and (bottom-right) mammal attacks.

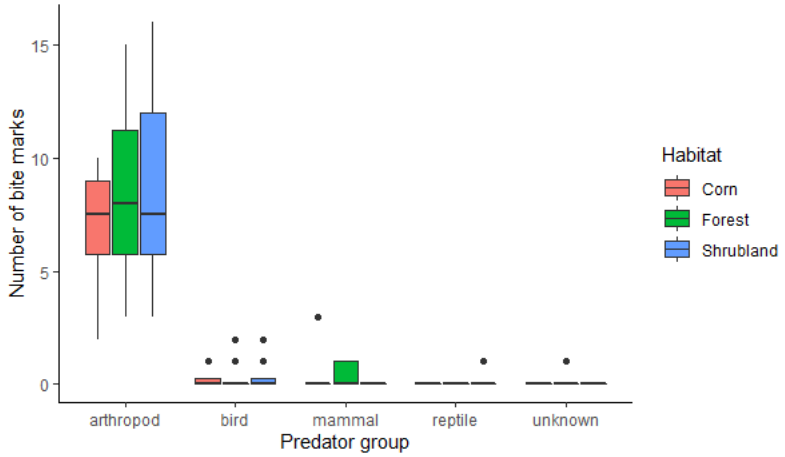


Figure a.8. Groups of the caterpillar predators in different habitats (n=315). Apart of the arthropod group, caterpillar predators in other groups are not considered in the further analysis in Chapter 3.

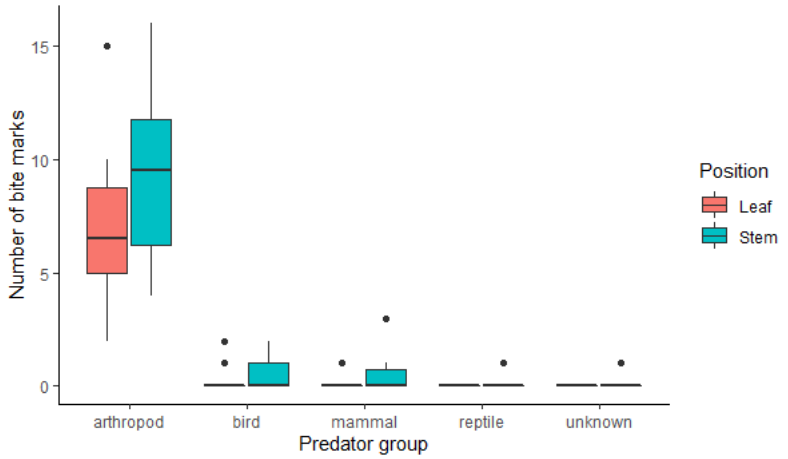


Figure a.9. Caterpillar predators in different positions (n=315).

g. Litter decomposition comparison in the primary and regenerated forests.

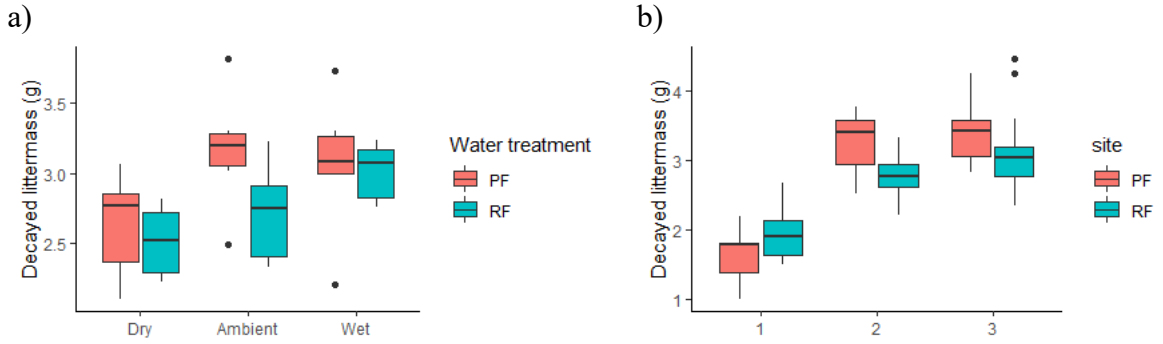


Figure a.10. Litter decomposition in (a) the mesocosm setting (litter invertebrate community were transplanted to the mesocosm) and (b) in-situ was similar between primary and naturally regenerated forests

Litter decomposition measured in the mesocosm experiment set-up was started by exposing litter bags containing leaf litters in the ground of the primary and naturally regenerated forests to let natural litter invertebrate community colonising the leaf litter. After one week of the exposure, leaf litters from each litterbag were retrieved and placed in the soil-containing flowerpots. Three levels of the rainfalls were treated to the mesocosm set-up by adding water to maintain the desired humidity levels (See Chapter 4). After one-week, remaining litter mass was dried under sunlight and weighted to obtain their dry mass.

For the in-situ measurement of the litter decomposition, litterbags were placed in the ground of the primary and naturally regenerated forests. After one-, two-, and three-week of the exposure, leaf litters from the subsets of litterbags were retrieved, dried under sunlight and weighted to obtain their dry mass. Litter decomposition under changing rainfall and under different temporal scale did not differ in the primary and naturally regenerated forests.

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Environmental Evidence

SYSTEMATIC MAP PROTOCOL

Open Access

What evidence exists on the relationship between agricultural production and biodiversity in tropical rainforest areas? A systematic map protocol

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Abstract

Background: Agriculture produces food for billions of humans and creates livelihoods for farmers. However, the current food production systems, driven by the increasing food demand and the ever-growing human population, are undermining ecological resources, primarily those related to biodiversity. Accordingly, agricultural production in tropical rainforest countries has been a trade-off, as regions harbor high biodiversity while also being pressured by agricultural land expansion. Consequently, threats to biodiversity are inevitable and will likely affect the ecosystem service provisions necessary for the agricultural process. Presently, no study reviews and maps the evidence of relationships between biodiversity and agriculture in the tropical rainforest landscape. Therefore, such a study is necessary to identify the knowledge gaps and provide scientific evidence to the relevant policymakers for safeguarding biodiversity within agricultural policies. This study aims to collect available published literature that evaluates the relations of agricultural production and biodiversity. We will focus on the agriculture and priority crops in the countries producing the commodities situated in the tropical rainforest landscape.

Methods: Generic search terms derived from research question elements will be used to search relevant articles. These terms are in English, and the searches will encompass global tropical rainforest countries. Peer-reviewed and gray literature articles retrieved from search engines and databases will be screened first using the title and abstract and second at the full-text level. The latter screening process will involve data coding to retrieve relevant characteristics from each eligible study and finally collate these characteristics into an evidence map, which will provide a current state of knowledge and further support evidence-informed policy formulation. The map presentation in the final report will also be complemented by a narrative synthesis explaining the trends, pinpointing the knowledge gluts and gaps, serving relevant information, and searchable databases for associated stakeholders.

Keywords: Food production, Rainforest, Farming practices, Agroecosystem, Natural ecosystem, Flora, Fauna, Services, Disservices, Evidence-based study

Background

Tropical forests occupy merely 45 percent of the total global forest area [1] or approximately 13 percent of the global land area [2] but provide habitats for two-thirds of the global terrestrial biodiversity [3]. Nevertheless, the degradation of tropical forests is a leading factor in the depletion of global biodiversity [4]. Furthermore,

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deforestation is driven mainly by agriculture [5], especially in tropical regions [6]. Almost 6 million hectares of tropical forests have been planted for agricultural purposes [7].

Managing tropical landscapes sustainably remains a substantial challenge [8]. On the one hand, conserving tropical biodiversity is undoubtedly important as tropical regions are prioritized global areas for conservation and restoration [9–12]. On the other hand, the agricultural landscape is important because it supplies foods to sustain rural livelihoods and nourish the human population [8]. As such, the demand for agricultural production to provide food and generate income is rapidly increasing in conjunction with human population growth. As the human population is projected to reach 11 billion this century [13], an increase in agricultural production is necessary primarily by expanding agricultural land.

However, as agriculture has developed quickly globally, concern about the impact of agriculture on the environment is increasing. For example, 99% of the global consumptive freshwater footprint is used for agriculture [14], while water itself is essential for human beings. Moreover, maximizing monoculture plantations and crop protection from pests in agricultural production requires crop interventions, such as pesticide use [15]. Hence, even though pest management can be naturally provided by ecosystem service-related biodiversity [16, 17], intervention using chemical pesticides is preferred given the costs, results, and effectiveness [18]. Consequently, the direct effects on wild species important for agricultural production are unavoidable. It seems likely that there is an endless loop where crop interventions create side effects on the environment, while more intense crop interventions are required in an altered environment. Hence, integrating natural ecosystem services into agricultural production is key to terminating the loop and sustaining agriculture [16, 19].

Fewer environmental regulations are one of the factors driving driven forest-rich tropical countries to increase agricultural demand [20]. Accordingly, regulations and policies for biodiversity and nature-friendly agriculture require methods and indicators for assessing the effects on both biodiversity conservation and function [15]. Currently, sustainable agriculture certification standards can integrate biodiversity protection and social justice despite the uncertainty in maintaining long-term sustainability. Good governance and regulatory frameworks are required to replace imperfect certification standards [19]. To establish relevant policies for agriculture and biodiversity sustainability, the Organization for Economic Co-operation and Development (OECD) has developed an Agri-Biodiversity Framework consisting of essential indicators to assess the link between agriculture and biodiversity [21]. However, this framework is not fully relevant in the tropical context and does not fully apply to tropical agriculture and biodiversity relationships. Therefore, understanding the bidirectional linkages between tropical agricultural production activities and biodiversity and collating this evidence are necessary. This approach will provide clearer information and identify the cutting-edge research on the matter; additionally, it could help inform decision-makers in transforming crop production systems in tropical agriculture.

Biodiversity and agricultural production can have a bidirectional relationship. There are biodiversity impacts on agricultural production and agricultural production impacts on biodiversity.

Impacts of biodiversity on agricultural production

Agroecosystems rely on the ecosystem services that natural ecosystems offer, such as pollination, pest control services, soil structure, and fertility regulation, and hydrological services [16, 22]. These ecosystem services are associated with biodiversity [23]. The role of biodiversity in improving agricultural production used to be neglected despite its high economic value. For example, the production of more than 75% of globally important crops and 35% of the food produced rely on pollination services [24]. The global value of crop pollination services is estimated to range widely from US$195 billion to ~ US$387 (US$267–657) billion annually [25]. However, pesticide misuse potentially reduces the number of pollinators in agroecosystems [26] and has economic impacts. Additionally, biodiversity can also reduce agricultural productivity through ecosystem disservices, such as pest damage, competition for water from other ecosystems, and competition for pollination [22]. Crop pests, pathogens, frugivores, and seed eaters are some of the components of biodiversity that could reduce agricultural production. Similar to ecosystem services, ecosystem disservices are triggered by the mismanagement of agroecosystems. Excessive pesticide use is likely to enable pest outbreaks and pesticide resistance [22]. Therefore, the ecosystem services and disservices provided by biodiversity are determined by agroecosystem management.

Impacts of agricultural production on biodiversity

Although highly relying on the ecosystem services provided by the biodiversity components, some agricultural practices negatively affect biodiversity, one of which is through habitat loss and fragmentation [27]. Moreover, among all other human activities, farming has created greater impacts on biodiversity [5], especially in tropical regions where most agricultural land is obtained by destroying tropical forests [6, 20]. Further, almost 6 million hectares of tropical forests were converted for

agricultural purposes annually in 1990 [7]. For example, forest conversion into croplands, especially for oil palm and rubber, drives the ongoing biodiversity crisis in Southeast Asia [28]. However, sustainable tropical landscape management could also help biodiversity thrive in agroecosystems. As such, designing well-managed agricultural landscapes can support many types of wild biodiversity, with neutral or even positive effects on agricultural production and human wealth [29]. Therefore, effective management of human-modified landscapes determines the fate of tropical forest biodiversity [3], whether biodiversity coexists with agroecosystems or vice versa.

Framework development

We developed a new framework called the Tropical Agriculture and Biodiversity Framework (TABF) [30] adapted from the OECD's agriculture-biodiversity framework [21]. The OECD framework is an existing comprehensive framework containing a set of agri-environmental indicators that assess agri-biodiversity relationships and the socioeconomic interactions between farming and biodiversity to achieve sustainable agriculture.

Similar to the OECD framework, in building the TABF, a series of meetings and workshop series were conducted by involving experts from various relevant universities or institutions in Indonesia and the UK. The newly generated framework, TABF, consists of five indicators related to agriculture and biodiversity, as well as external drivers, i.e., socioeconomic factors and disturbances (Fig. 1, Table 1). As external factors in the TABF, socioeconomic factors and disturbances interact with the indicators to different extents. Hence, these will be explained by merging them into the relevant indicators. Below is the explanation of each indicator as well as the important elements included in it.

Tropical agricultural production base

An agricultural production base is defined as the compulsory necessity for running agricultural production.

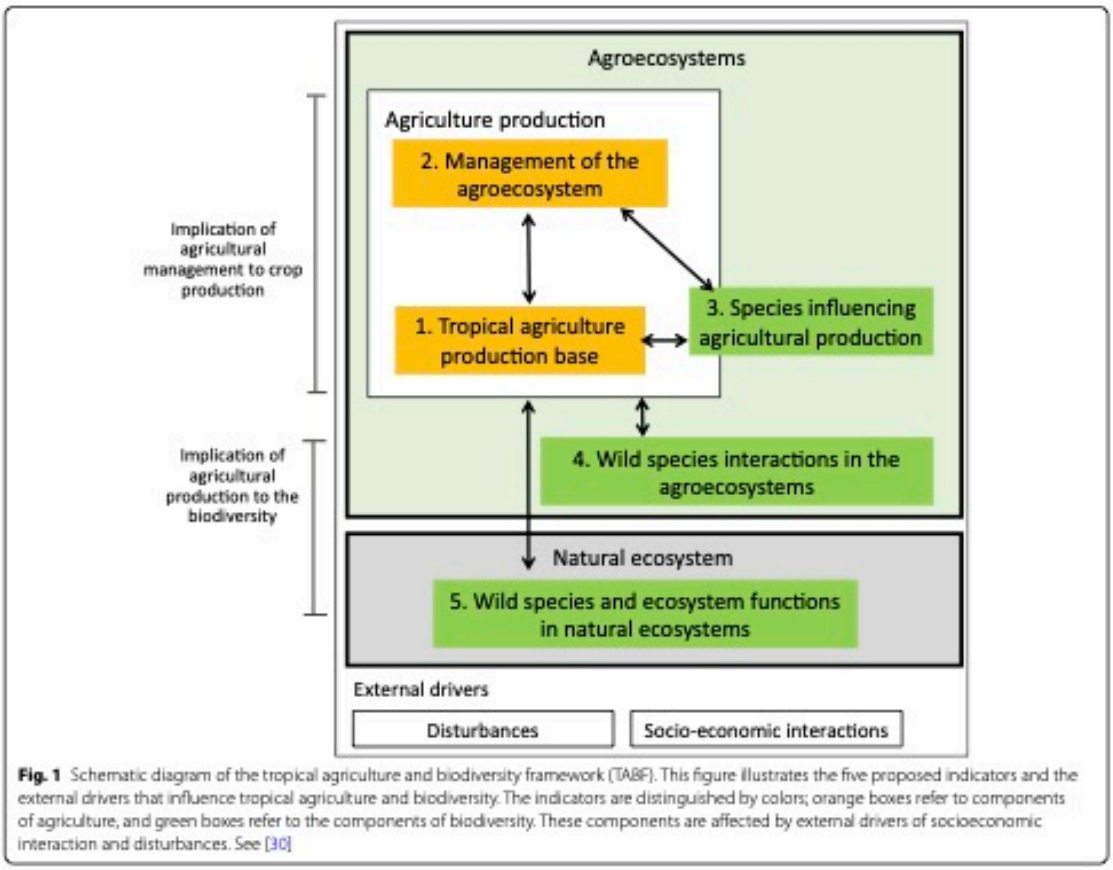


Fig. 1 Schematic diagram of the tropical agriculture and biodiversity framework (TABF). This figure illustrates the five proposed indicators and the external drivers that influence tropical agriculture and biodiversity. The indicators are distinguished by colors; orange boxes refer to components of agriculture, and green boxes refer to the components of biodiversity. These components are affected by external drivers of socioeconomic interaction and disturbances. See [30]

Table 1 A summary of all indicators and sub-indicators in the TABF. From [30]

Indicators	Definition	Sub-indicators	Elements
Tropical agricultural production base	Compulsory necessity for agricultural production, both abiotic and biotic factors	Edaphic and climatic factor	Water availability, soil type or texture, soil nutrient, soil organic matter, hot and humid environment, and precipitation
		Genetic resources	Ecologically suitable seeds, quality of seeds, and crop life cycle
Management of agroecosystem	Either on-farm activities or intervention to manage biotic and abiotic factors in the agroecosystems	Habitat conversion to agricultural land	Primary tropical forest, and old-farmed or disturbed land
		Farm management practices	Soil management (soil tillage, sowing, and fertilizer amendment), pest management (pest predator, insecticide, fungicide, and herbicide), water management (irrigation, rainfed, and retention basin)
		Farming system	Monoculture and polyculture
		Farming scale	Small scale (smallholder agriculture, garden, subsistence farming) and large scale (industrial agriculture)
Species influencing agricultural production	A range of organisms that interact directly with agricultural production	Aboveground biodiversity	Plants (including invasive species), animals, fungi, and microorganisms that contribute to ecosystem services and disservices
		Soil biodiversity	Fungi, microorganisms, and invertebrates that contribute to ecosystem services and disservices
Wild species interactions in the agroecosystem	A range of organisms from surrounding ecosystems that utilize agroecosystem for multiple purposes	Human and wildlife interaction	Human and wildlife conflict, and illegal hunting
		Chemical exposure in agroecosystems	Contamination, and eutrophication
		Habitat change	Habitat fragmentation
		Spatial and temporal use of wildlife in the agroecosystem	Nesting, migration, breeding, foraging, and passing by
Wild species and ecosystem functions in natural terrestrial ecosystems	A range of organisms in natural habitats and ecosystems functions around agricultural production areas affected by agricultural activities	Biodiversity	Forest animals, forest mammals, mammals (arboreal primates, big cats, raptors, insectivores, frugivores, and other groups of mammals), and birds (canopy bird, etc.)
		Ecosystem functions	Microclimate, hydrological pattern

The tropical agricultural production base emphasizes the basic capitals of agricultural production that determine whether agriculture can produce a certain crop yield. This should be considered for maximizing crop yield potential while becoming a subject of agricultural production management. There are two main components of this indicator: edaphic and climatic factors and genetic resources.

Management of the agroecosystem

This is categorized as a group of indicators that signify habitat quantity and quality. Habitats in this study refer to agroecosystems and the surrounding natural ecosystems. For this indicator, we found the need to include information on land or natural ecosystem conversion to agricultural land. Furthermore, practices in agricultural management (i.e., soil, pest, and water) and farming systems are included since they reflect human interventions to biotic and abiotic resources.

Species influencing agricultural production

Identifying and understanding wild species in agricultural production will help us to better understand which taxa play significant roles in agroecosystem processes (both positive and negative) and how they interact within the agroecosystem. This includes how biodiversity affects agricultural management as well as agricultural production. Intensive agriculture production activities at the local scale have significant implications on surrounding wild species of flora and fauna (ecology) as well as economic impacts. Moreover, species capable of adapting to the agricultural environment as well as their species composition may be limited by management practices including soil, pest, and water management (as mentioned in the previous section). Exploring the interaction pathways between biodiversity and agricultural production is the combination of many key elements within the agroecosystem.

Wild species interactions in agroecosystems

Agroecosystems have direct and indirect impacts on natural ecosystems. Wildlife that lives adjacent to agricultural land is affected by these human-modified ecosystems. With proper management, humans and wildlife can coexist together and utilize closely entangled areas. In the TABF, we will incorporate how agroecosystems support the species that require and use these agroecosystems and, conversely, the disruption caused by poorly managed agroecosystems towards these species. We also include the wildlife status (from the most concerned to the least concerned), but generally, we want to see how wild species in the agroecosystems use and require the aforesaid. The proposed sub-indicators include the spatial and temporal uses of wildlife in the agroecosystems, human and wildlife interactions, chemical exposure in the agroecosystem, and habitat change.

Wild species and ecosystem functions in natural ecosystems

This particular indicator includes how agroecosystems support the species in the natural habitat and the negative impacts that on-farm and agroecosystem management actions cause. In general, we want to see what relationships exist between all kinds of species that use natural habitats and agroecosystems. In addition to the diversity of plants and animals at the species level, we look at the ecosystem level and the functions attached to it.

External drivers

External drivers refer to disturbances and socioeconomic interactions. Agricultural practices with the ecological dynamics occurring therein greatly depend on environmental conditions ranging from climate varieties, temperature fluctuations, fires, precipitation, and droughts. Regarding the disturbances, we focus on natural disturbances independent of agricultural practices: volcanic eruptions, hurricanes, and disease outbreaks among others. These natural disturbances, directly and indirectly, affect the sustainability of agricultural practices and biodiversity in the agroecosystem. In addition to ecological approaches in linking agriculture and biodiversity, factors such as social, economic, and policy are important in determining land-use decisions and farmers' attitudes towards agricultural practices, which in turn affect biodiversity. Socioeconomic interactions include land ownership, farmers' knowledge, and local wisdom. Governmental policies, such as national food security targets and transmigration programs, should also be considered.

The ultimate goal of developing the TABF is to conduct an evidence synthesis study (i.e., a systematic map and systematic review). In this paper, we focus on a systematic map study to collate the current state of evidence that shows the bidirectional linkages between agricultural production and biodiversity in the tropical rainforest landscape.

We will operationalize the framework into an evidence map matrix. Two evidence matrices will be built, one focusing on how agricultural practices affect biodiversity (Map 1) and the other focusing on how biodiversity contributes to agricultural production (Map 2). These matrices will be established after the review process and will be presented in the evidence map result report.

Furthermore, regarding the incorporation of the external drivers into these relationship map matrices, first, we selected the most salient and important drivers that influence agriculture and biodiversity. Second, we

Table 2 Selected indicators and sub-indicators of the TABF for systematic Map 1, the relationship between tropical agricultural production and biodiversity

Indicators	Key search terms derived from sub-indicators
Agricultural components as the exposure	
Tropical agricultural production base	Environmental factors
	Genetic resources
Management of the agroecosystem	Land conversion
	Socioeconomic factors
	Disturbances
	Soil management
	Pest management
	Water management
	Land ownership
	Crop diversification
Biodiversity components as the outcomes	
Species influencing agricultural production	Aboveground biodiversity
	Soil biodiversity
Wild species interactions in the agroecosystem	Spatial and temporal uses of wildlife in the agroecosystems
	Human and wildlife interaction
	Chemical exposure in agroecosystems
	Habitat loss & fragmentation
Wild species and ecosystem functions in natural ecosystems	Wild species and ecosystem functions in natural ecosystems

determined which indicators in the TABF were relevant to explain each driver. Socioeconomic interactions will likely be relevant to indicator two (management of agroecosystems), while disturbances will affect most indicators to different extents. Therefore, by integrating these drivers into the relevant indicators, we expect to see how these drivers interact and influence agricultural practices and biodiversity.

Additionally, for a relationship map of agricultural impacts on biodiversity, the included sub-indicators are displayed in Table 2. The included sub-indicators that describe the linkages between biodiversity and tropical agriculture are shown in Table 3. For data collection purposes, we modify the terminology of each sub-indicator with the relevant and illustrative key search terms.

Objective of this review

This systematic map aims to assemble and map the present state of evidence that describes the linkages of agricultural production activities and biodiversity in tropical rainforest landscapes. Moreover, we are particularly interested in the bidirectional relationships between tropical agricultural production and biodiversity.

In light of the above, undertaking a systematic map of evidence on those two subjects is necessary, as no such study has yet been performed, particularly in tropical rainforest countries, where the majority of important,

Table 3 Indicators and sub-indicators of the TABF included in systematic Map 2, the relational evidence of the biodiversity implications to tropical agriculture

Indicator	Key search terms derived from sub-indicators
Biodiversity components as the exposure	
Species influencing agricultural productions (based on services and disservices)	Shelter
	Microhabitat
	Litter sources
	Invasive species
	Pollinator
	Pest predators
	Decomposer
Wild species interactions in the agroecosystem	Avifauna and insects
	Terrestrial mammals
Tropical agricultural production base	Genetic resources
Agricultural components as the outcomes	
Tropical agricultural production base	Environmental factors
	Crop varieties
Management of the agroecosystem	Socioeconomic factors
	Soil management
	Pest management
	Water management
	Crop diversification

high-economic value crop commodities are produced [31]. Furthermore, almost all the systematic map papers on the related subject we found undertaking this review focused on a very narrow scope of agricultural matters and were not specific to the rainforest landscapes. For instance, Van Der Meer et al. [15] mapped the evidence of fruit orchard impacts on biodiversity indicator species groups in temperate climates; Shin et al. [32] conducted a systematic map study on agroforestry practices in the Asia–Pacific region.

Hence, we aim to conduct a systematic map study that captures agricultural activities at the multi-spatial scale and identify their relations with biodiversity in tropical agroecosystems and natural ecosystems. We will include the diversity of flora and fauna at the species and ecosystem levels along with the ecosystem services and disservices they provide to agricultural activities.

By doing so, it is expected that the evidence maps of agriculture-biodiversity and the vice versa relations in tropical rainforest contexts will provide a clearer overview of the current state of research and highlight the trends on that subject. Additionally, the evidence map outcome would help to inform related stakeholders to better develop science-based policies of sustainable food production.

The primary research question that will overarch this systematic map study is therefore as follows:

What evidence exists on how tropical agricultural production activities and biodiversity influence one another?

Following that, the secondary research questions are as follows:

1) *What is the state of evidence for tropical agricultural production and its relations to biodiversity in terms of the quantity of articles, study types, commodity types, and geographical locations?*
2) *What evidence exists regarding the impacts of tropical agricultural production bases and the management of agroecosystems on biodiversity?*
3) *What evidence exists regarding the impacts of biodiversity on tropical agricultural production?*

Elements of the primary question

Given the bidirectional linkages we intended to assess, we identified two different key elements of the primary question based on secondary research questions two and three outlined as follows:

2) What evidence exists regarding the impacts of tropical agricultural production bases and the management of agroecosystems on biodiversity?

Population: Tropical rainforest areas.

Exposure: Tropical agriculture production base and management of the agroecosystem.

Comparator: No agriculture (spatial) or before agriculture (temporal).

Outcome: Changes in indicators (e.g., species richness, abundance, composition, density) of biodiversity in agroecosystems and natural ecosystems.

3) What evidence exists regarding the impacts of biodiversity on tropical agricultural production?

Population: Agriculture producing priority crop commodities in tropical rainforest countries.

Exposure: Existence of biodiversity (e.g., species richness, abundance, composition, and density) and mediated functionality (i.e., ecosystem services/disservices) in agroecosystems.

Comparator: Farms with less biodiversity mediating functionality.

Outcome: Changes of tropical agricultural production base (i.e., availability of edaphic and climatic factors and availability and suitability of crop varieties) and changes in the suitability of the agroecosystem management (i.e., management of soil, water, pest, and crop diversification).

Methods

This study will follow guidance on conducting a systematic map of evidence according to the Collaboration for Environmental Evidence [33].

Searching for articles

Key search terms

We established generic key search terms using the English language to answer the research questions. The initial search terms generated were related to elements of the primary research questions: "tropical rainforest agriculture" AND "biodiversity." These terms were then developed for the establishment of search strings by looking at the synonyms or alternative words commonly used within the topics. We are aware that all search terms produce some irrelevant articles; however, we would like to ensure that the search strings capture as comprehensive as possible articles relevant to the research questions by developing and refining the strings through iterative pilot testing in Scopus.

Moreover, as we are interested in observing the distinguished nature of bidirectional relations between tropical agriculture and biodiversity, we proposed two different exposure and outcome terms according to the secondary research questions as follows:

For the second secondary research question:

Map 1

Subject terms "rain forest" OR "rainforest" AND "tropic*" OR "humid" OR "moist" OR "equator*".

Exposure terms "agri*" OR "agro*" OR "farm*" OR "crop*" OR "horticulture" OR "food produc*" OR "cultivat*" OR "yield produc*".

Outcome terms "species" OR "wildlife" OR "plant" OR "plant*" OR "fauna" OR "flora" OR "animal" OR "insect" OR "insect*" OR "microb*" OR "microorgani*" OR "bacter*" OR "fung*" OR "invertebrate" OR "pollinat*" OR "mammal" OR "bird" OR "livestock" OR "invasi*" OR "divers*" OR "biodiversity" OR "group*".

Adjacent to "rich" OR "rich*" OR "even*" OR "abundan*" OR "change" OR "dynamic" OR "functio*" OR "conflic*" OR "interac*" OR "distur*" OR "alter*" OR "decline" OR "decrease" OR "reduc*" OR "loss" OR "contraction" OR "increase" OR "gain" OR "grow*" OR "restor*" OR "expansion" OR "effec*" OR "affec*" OR "respon*" OR "relatio*" OR "influenc*".

For the third secondary research question:

Map 2

Subject terms "rain forest" OR "rainforest" AND "tropic*" OR "humid" OR "moist" OR "equator*".

Exposure terms "role" OR "effect" OR "impact" OR "contribution" OR "function" OR "relationship".

Adjacent to "species" OR "wildlife" OR "plant" OR "plant*" OR "fauna" OR "flora" OR "animal" OR "insect" OR "insect*" OR "microb*" OR "microorgani*" OR "bacter*" OR "fung*" OR "invertebrate" OR "pollinat*" OR "mammal" OR "bird" OR "livestock" OR "invasi*" OR "divers*" OR "biodiversity" OR "group*".

Outcome terms "agri*" OR "agro*" OR "farm*" OR "crop*" OR "horticulture" OR "food produc*" OR "cultivat*" OR "yield produc*".

Adjacent to "management" OR "practice" OR "soil" OR "water" OR "irrigation" OR "pond" OR "pest" OR "pesticide" OR "weed" OR "farming system" OR "monoculture" OR "polyculture" OR "agroforest" OR "intercrop*" OR "small-scale" "large-scale" OR "industr*".

The above exposure and outcome search strings were applied in the tested database and will be operated in the targeted databases to search for articles. Notably, as the different database sources might have different search functionalities, modest string modifications using the Boolean operators may be necessary. The record of the tested search strings that also represent the result of scoping exercise can be found in Additional file 1. In Scopus, 84 and 52 search strings for Map 1 and Map 2 were examined respectively. The final strings tested in Scopus with year limitation > 2015 for Map 1 resulted in 432 hits, and Map 2 resulted in 219 hits. The search strings tested in Scopus sufficiently resulted in hits assessing the impacts of tropical agriculture on biodiversity, and conversely, the impacts of biodiversity on tropical agriculture. The use of "rainforest" and "tropic" terms combined with its synonyms and syntax features helped narrow the results captured in the test search. The hits capture articles that quantify the variety of exposures and measured outcomes listed in our eligibility criteria. The agricultural exposure types captured in the test search of Map 1 including land-use gradients, land conversion into crop plantations, crop diversification (e.g. monoculture and agroforestry), pest management, and soil management. The types of biodiversity outcomes measured include soil biodiversity (e.g. microbe, fungi, and dung beetle), and aboveground biodiversity (e.g. butterfly, bat, epiphyte, and mammal). The test search for Map 2 results biodiversity exposures ranging from genetic resources, crop varieties, trees as litter source, pest predators, and pollinators. Examined agricultural outcomes include ecologically suitable seeds (e.g. drought resistant cultivars), soil organic matter, soil water content, and pest control.

Estimating the comprehensiveness of the search

To examine the sensitivity and whether these search strings cover relevant papers, we ran the strings against a set of test libraries (Additional file 2). The test libraries, which were independent from the test search results, were identified through asking researchers judged by our understanding on the conceptual framework and eligibility criteria and by looking at bibliographic list from currently available review studies on similar topics. All the citations listed in the test library were captured by using the keywords we established in the test search.

Searching the literature

Publication bibliographic databases

We will undertake a literature search process using publication databases and organizational websites. The publication databases used to collate peer-reviewed articles, including multidisciplinary and publisher databases, are described as follows:

1. *Multidisciplinary bibliographic sources:* including Scopus, Web of Science Core Collection list of indexes provided in Additional file 1, Directory of Open Access Journals (DOAJ), Science Publishing Groups, AGRICOLA National Agricultural Library, and Citation Database, AGRIS Agricultural Science and Technology Information Systems
2. *Publisher databases:* Elsevier's ScienceDirect, Wiley InterScience, and Springer Link

Gray literature

In addition to peer-reviewed articles, we decide to include gray literature, not only because it is suggested by the CEE guidelines [33] but also because it is useful in minimizing publication bias and collecting relevant articles probably not published in common peer-reviewed bibliographic sources [34]. However, as searching and assessing gray literature can be time- and resource-consuming [35], we will search articles from the obtained gray literature databases relevant to the study objectives. Relevant gray literature articles will be compiled, screened, and synthesized as peer-reviewed articles.

The types of gray literature included working papers, proceedings, theses, dissertations, policy briefs, and reports [23]. This literature will be searched through organizational databases (i.e., universities repositories, nonprofit organizations, and governmental institutions) and subject-related particular websites, as shown in Table 4.

Web-based search engines

Google Scholar will be utilized to supplement the search process, expected to increase the chance of obtaining relevant papers that might not yet be captured in the other publication sources used in this study [36].

Accordingly, article searching in the peer-reviewed and gray literature mentioned above will be confined by the time of publication. Based on our interest, we will account only for articles published in the years $\geq$ 2000. There are several considerations when deciding the cut-off date for this study. First, we want to get enough papers to synthesize evidence and draw a conclusion by having a span of 20 years. Second, the result of the search test was limited to years before 2000 (1979–1999) in Scopus, which produced few articles. The paucity of articles published in these periods may have been influenced by article digitization technology, which was not as advanced as the year 2000 and beyond. Moreover, most of these results did not meet our eligibility criteria, either in terms of the exposure/outcome or the type of article.

Bibliographic management

The articles obtained from the database searching will be assembled in Mendeley, a reference management software helpful in assisting the reviewers with organizing hundreds of thousands of references so that eligibility screening can be performed efficiently.

Article screening and study inclusion criteria

Eligibility screening

Collected citations and articles from the databases will be stored in the Mendeley desktop library. The next process will be assisted by Colandr, a machine learning software developed by Cheng et al. [37]. It consists of two systems: Firstly, the user screens the titles and abstracts. Results of the first screening that can be included, excluded, or

Table 4 List of organizational databases to be used for searching gray literature

Organizational databases	Web URL
Bioversity International	https://www.bioversityinternational.org/
Center for International Forestry Research (CIFOR)	https://www.cifor.org
Climate Change Agriculture and Food Security (CCAFS)	https://ccafs.cgiar.org/publications/
Consultative Group for International Agricultural Research (CGIAR)	https://ciat.cgiar.org/publications/ciat-library-resources/
Ecoagriculture Partners	https://ecoagriculture.org/resources/publications/
Food and Agricultural Organization	https://www.fao.org
French Agricultural Research and International Cooperation Organization for The Sustainable Development of Tropical and Mediterranean Regions	www.cirad.fr
International Development Research Centre (IDRC)	https://www.idrc.ca/en
International Food Policy Research Institute Library (IFPRI)	http://library.ifpri.info/
International Institute of Tropical Agriculture (IITA)	https://www.iita.org/knowledge/publications/
International Impact Initiative (3ie)	https://www.3ieimpact.org/evidence-hub/publications
International Institute for Environment and Development (IIED)	https://pubs.iied.org/
South Asian Network for Development and Environmental Economics (SANDEE)	http://www.sandeeonline.org/publicationdisp_main.php
The Economics of Ecosystems and Biodiversity	http://teebweb.org/publications/
TROPENBOS Sustainable Land Use	https://www.tropenbos.org/resources/publications?theme_title=Sustainable+land+use
Tropical Agricultural Research and Higher Education Center (CATIE)	http://www.catie.ac.cr/en/
World Resources Institute (WRI)	https://www.wri.org/publication
CABI Agriculture and Bioscience	http://www.cabdirect.org/

unknown will be learned by machine learning to rank the remaining and unscreened citations based on their relevance. The more machine learning is trained, the more it learns and puts the most relevant citations at the top of the list. At the data extraction in system 2, machine learning is trained from the first 25 pdf documents manually screened and categorized by users. The model will learn relevant keywords and henceforward will automate the data extraction process by displaying only keywords in the category that the user needs. Users can label the recommended information by accepting, rejecting, and skipping them in system 2.

We will import the collected articles into Colandr, and the software will remove duplicates. Subsequently, the articles will be screened first at the title and abstract levels by two reviewers. The reviewers will screen and evaluate the same set of articles independently but will ultimately compare the results to test the consistency. If there is a dissensus between the reviewers, a discussion to reach an agreement over the contentious article will be performed before the full-text screening is conducted.

The following stage will be the second screening at the full-text level. The full text will be reviewed against the same inclusion and exclusion criteria as in the first-stage screening. To increase consistency and reliability, reviewers will also be responsible for dual and independent screening of articles. The excluded articles will be reported in additional files in the narrative report with justifications for excluding them. Articles that pass full-text screening will be extracted to answer the research questions. The screening and extraction steps are applied to produce Map 1 and Map 2, respectively. To test Colandr's accuracy at the data extraction stage, we will pick at least 25 articles (outside the first 25 pdf manually-extracted documents) highly relevant to the study and compare whether Colandr's label recommendation match with these 25 papers.

Eligibility criteria

The eligibility criteria explained below are used to screen the articles that explain the impacts of tropical agriculture on biodiversity and the opposing relations of biodiversity to agriculture. Hence, we proposed different exposures, outcomes, and comparators to explain those bidirectional linkages. The remaining elements, such as populations and study design, were the same.

Relevant populations

The key criteria we will use in this population relate to agricultural activities that produce priority crop commodities in tropical rainforest countries. Among the top priority crop commodities we retrieved from the FAO list (based on its average gross production value) are dominated by food crops (Additional file 3): rice, soybeans, maize, sugar cane, wheat, oil palm, oil palm fruit, cassava, bananas, seed cotton, vegetables, mangoes, mangosteens, guavas, potatoes, cotton lint, tomatoes, oranges, coffee, yams, rubber, beans, onions, plantains, chilies and peppers, okra, groundnuts, pineapples, chickpeas, papaya, avocado, lychees, durian, rambutan, passionfruit, coconuts, grapes, cacao, clove, and tobacco [38]. Additionally, we compared the FAO's commodities list with a priority commodity list from one of the key tropical countries in this study as a reference: Indonesia's Ministry of Agriculture Strategic Plan [39]; we found that these lists intersect. Substantially, we will exclude tropical rainforest agriculture whose activities are in the form of livestock, aquaculture, pasture, mariculture, silvofishery, urban agriculture, riparian ecosystem agriculture, and agriculture producing biofuel, medicine, timber, fiber, and fodder.

Relevant tropical rainforest types: We will include studies that investigated agriculture and food crop production in tropical rainforests or equatorial rainforests or humid forests. Within this scope, we will incorporate studies ranging from pristine forests or naturally grown forests adjacent to agroecosystems. Moreover, as the types of natural ecosystems in the tropics are ample, of interest, we will focus only on the terrestrial part in which the classification follows differentiation based on physical (i.e., soil, climate, and altitude) and physiognomic characteristics. These include lowland evergreen rainforest, semievergreen rainforest, lower montane rainforest, and upper montane rainforest in tropical countries [40, 41]. The distinguishing characteristics of these rainforest ecosystem subtypes are summarized in Table 5.

Regarding the spatial scale, we considered including a local (field or farm) landscape. This was suggested by previous research that investigated the effects of agriculture on biodiversity at multiple scales [42, 43] and based on discussion with Indonesian biology experts.

Relevant exposures, comparators, and outcomes

As we will assess bidirectional interactions between agriculture and biodiversity, we will generate two maps: (1) evidence of agriculture towards biodiversity (or Map 1) and (2) evidence of biodiversity towards agriculture (or Map 2). Therefore, we will have two sets of relevant exposures, comparators, and outcomes as follows:

(1) Evidence of agriculture towards biodiversity (Map 1).

Relevant exposures: For exposure, we will include indicators and sub-indicators of the tropical agricultural production base (environmental factors and genetic resources), land conversion, socioeconomic interactions, disturbances, and management of soil, pests, and

Table 5 Four types of rainforest ecosystems distinguished by the altitude and physiognomy of the vegetation layer [40, 41]

Rainforest types	Altitude	Physiognomic properties
Lowland evergreen rainforest	From sea level to 1200 m	Thick closed-canopy stands. Evergreen trees in a minimum of 3 layers. Canopy surpassing 30 m. Emergent layer surpassing 45 m in height. Lack of plant species diversity. Rare floor vegetation and are dominated by tree seedlings
Montane rainforest		
Lower	Altitude range is 1200–1500 m	Canopy is more equal. Lower statured compared to lowland evergreen. Canopy height 15–33 m
Upper	Altitude range is 1500–4000 m	Smallest in stature. Emergent trees maximum 26 m. Canopy height from 1.5 to 18 m
Semi-evergreen rainforest	From the sea level to approximately 1000 m. Strongly influenced by a yearly humidity level	Tall closed-canopy. Canopy and emergent heights are less than lowland evergreen. Emergent vegetation can reach 45 m in height

water in the agroecosystem. In addition, a farming system that entails the scale of land ownership (smallholders and large holders) and crop diversification (monoculture and polyculture) will be included. We will exclude an integrated agricultural system (i.e., livestock combined with cropland), greenhouse agriculture, organic agriculture, hydroponics, verticulture, and silviculture. Further details on the framework-selected agricultural exposures included in this study are shown in Table 2. In terms of the spatial scale, we will cover studies that assess agricultural practices not only on a field and farm basis but also on a multilevel scale such as subnational, national, and regional scales.

Relevant comparators: The comparator includes a spatial and temporal comparator. Spatial comparator in empirical or experimental studies comprises of land with or without the agricultural interventions, and studies comparing natural or secondary forest versus farms with the interventions. Furthermore, studies comparing the similar type of crop agriculture in different locations (field, region, or country) will also be considered. The comparisons include different agroecosystem management methods applied by farmers (e.g., soil tillage vs chemical fertilizer amendment, polyculture with timber vs spice trees, pest management with natural fallows vs planted fallows, etc.). Temporal comparators examine the difference in outcomes before and after an agricultural intervention.

Relevant outcomes: Following the agricultural exposures that we will examine in this study, we will include the changes in biodiversity indicators (e.g., species richness and abundance) in the agroecosystems and natural ecosystems as the outcomes (see Table 2).

(2) Evidence of biodiversity towards agriculture (Map 2)

Relevant exposures: For the opposing relations, the focus of exposure would be biodiversity elements that offer services or disservices to agriculture. These will include environmental factors and genetic resources. It also comprises indicators of flora and fauna influencing agricultural production consisting of aboveground and soil biodiversity. The former includes plants that provide shelter, microhabitat, and litter sources. Invasive species, pollinators, and pest predators will also be included. Soil biodiversity consists of decomposers. Additionally, relevant spatial scales for exposure are at a multilevel scale because, in the TABF, we clearly distinguish biodiversity in the agroecosystem and natural ecosystem surrounding the farmland.

Relevant comparators: We will compare farms with more or less biodiversity mediating functionality.

Relevant outcomes: Changes of tropical agricultural production base (i.e., availability of edaphic and climatic factors, and availability and suitability of crop varieties) and changes in suitability of the agroecosystem management (i.e., management of soil, water, pest, and crop diversification) (Table 3).

Relevant study designs

The articles that will be included are grounded empirical studies employing qualitative, quantitative, or a combination of both types. Extensively, we will also consider studies of systematic reviews, reviews, and research that use experimental, quasi-experimental, and empirical modeling methods. Finally, we will exclude studies conducted using theoretical or nonempirical modeling studies, solely qualitative research, philosophical, conceptual, editorials, and books.

Study validity assessment

A systematic map of evidence does not require any formal validity and quality assessment for the included papers [33]. However, these assessments are necessary if subset research in the form of a systematic review is

conducted. Since our main research intention is to create a systematic map, we will not apply study validity assessment considering the anticipated volume of studies we may collect. However, we will record the information related to the study context (in situ or ex situ) and study type/design (observational or experimental) of the included articles. We acknowledge that this will likely impair and limit our interpretations of the evidence map; therefore, we will communicate this limitation as part of our final report.

Data coding strategy

As required in RepOrting standards for Systematic Evidence Syntheses (ROSES, Additional file 4), a predesigned data collection coding sheet was made prior to the study (Additional file 5) and will be filled during the data extraction stage. The coding tool was developed based on similar studies [15, 44] with adjustments to meet our needs. To anticipate a large number of articles needed to be extracted, one person is assigned to extract one article. Furthermore, to ensure that this conduct still maintains the CEE standards and equally ensures consistency among reviewers, cross-checking towards the number of samples of extracted articles will be carried out. However, any resulting discrepancy encountered among the reviewers from this cross-checking will be addressed, discussed, and agreed upon for consistency. The data extracted from each study will include the following information:

- Source of publication
- Bibliographical information
- Publication type
- Study content
- Geographic location of the study
- Rainforest type
- Exposure type
- Outcome type
- Farm produce
- Study design
- Type of comparator
- Farm ownership

Study mapping and presentation

The visual representation of the maps in two structured matrices of the evidence depicting the bidirectional relationships between agricultural management and biodiversity aspects will be established. This approach will allow us to highlight the areas of studies with plentiful evidence or the lack thereof. Moreover, a descriptive statistical analysis to encapsulate the key characteristics and depict the trends along with the narrative synthesis will be performed. The key characteristic presentations will depend on the articles that pass the screening but presumably contain information about the population, exposures, outcomes, countries of study, and types of commodities examined.

Supplementary Information

The online version contains supplementary material available at https://doi.org/10.1186/s13750-021-00233-z.

Additional file 1. Search strings tested in Scopus.

Additional file 2. List of publications in the test library that meet the inclusion criteria.

Additional file 3. List of agricultural priority commodities in tropical rainforests countries.

Additional file 4. ROSES for systematic map protocols. Version 1.0.

Additional file 5. Coding sheet for Map 1 and Map 2.

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Authors' contributions

SM conceived the idea of a systematic map study and secured funding support. All authors provided conceptual and technical information on the scope of the study and design of the search strategy. VA developed inclusion/exclusion criteria with input from MH, FO, SM, and CS. CS implemented and refined the search strategy with inputs from MH, FO, and VA. VA, CS, MH, and FO developed the data coding strategy. Further, FO will coordinate the data mapping process, analysis, mapping presentation, and narrative synthesis. VA, MH, FO, and CS co-wrote the manuscript. All authors read and approved the final manuscript.

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Availability of data and materials

The datasets used and/or analyzed during the current study are available from the corresponding author on reasonable request.

Declarations

Ethics approval and consent to participate

Not applicable.

Consent for publication

Not applicable.

Competing interests

The authors declare that they have no competing interests.

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Fourth decades of deforestation dynamics in Panua Nature Reserve and surrounding landscape, Sulawesi

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Abstract

Deforestation is the biggest challenge for tropical rainforests management in Sulawesi, Indonesia. It not only reduces forest cover but also threatens protected wildlife and all elements of forest biodiversity. The aims of this study are (1) to estimate the deforestation rate in Panua Nature Reserve (*Kawasan Suaka Alam*/KSA) and surrounding landscape that consists of limited production forest (*Hutan Produksi Terbatas*/HPT) and convertible production forest (*Hutan Produksi yang dapat Dikonversi*/HPK) (total 502.8 square kilometres) over four decades (1978-2018) and (2) to investigate its changing drivers. We used Landsat time-series data and Support Vector Machine (SVM) algorithm with Radial Basis Function (RBF) kernel to create three land cover maps (for 1978, 1996 and 2018). Each map has an overall accuracy value of more than 90% (kappa >0.9). These maps were then further analysed using the post-classification comparison method to examine forest cover changes. In the past four decades, deforestation totalled 6,482 hectares (162 ha/year), causing 13.4% forest cover loss. Deforestation of KSA accounted for 1,185 ha or 18.3% of the total deforested area, HPT 2,732 ha (42.1%) and HPK 2,566 ha (39.6%). The main driver of deforestation was agricultural expansion which accounted for 86.7% of the deforested area. The other interrelated drivers were new rural settlements, gold mining, and illegal logging. The government policies that allegedly triggered deforestation are transmigration and remote indigenous community (*Komunitas Adat Terpencil*/KAT) empowerment program, agricultural development through corn-based agropolitan, and altering the status of KSA to HPT and HPK through spatial planning. Another driver that naturally occurred is landslides. It was found in small quantities but contributed to deforestation. We suggest several strategies to reduce deforestation: building collaborative forest monitoring, improving village land through participatory land-use planning, resolving forest land conflicts through social forestry programs, increasing community awareness on conservation, and building capacity building on sustainable landscape management.

Keywords: Sulawesi, deforestation, transmigration, Support Vector Machine, social forestry

1. Introduction

Despite being home to some of the most threatened and exotic species on earth, the tropical rainforest has been massively degraded. Indonesia has one of the highest deforestation rates among tropical countries(Margono et al., 2014). In 1997, about 0.81 and 2.57 Gt of carbon (equivalent to 13–40% of the mean annual global carbon emissions from fossil fuels) that resulted from the burning of peat and vegetation forest in Central Kalimantan was released into the atmosphere (Page et al., 2002). From the 2000 to 2012 period, Indonesian primary forest loss totalled over 6.02 million hectares and increased on average by 47,600 ha per year (Margono et al., 2014). Deforestation causes a further spread of understorey plants, decreasing species number, tree density and habitat complexity (Nordhaus et al., 2019). It also destroys the habitat of endemic species such as Maleo (*Macrochepalon maleo*) (Butchart & Baker, 2000; Dekker, 1990) and *Tarsius pelengensis* (Supriatna et al., 2020) in Sulawesi, Bornean

orangutans (*Pongo pygmaeus*) (Voigt et al., 2018), and Sumatran tigers (*Panthera tigris*) (Linkie et al., 2008). On the economic and social aspects, deforestation reduced agricultural productivity by 45% between 2001 and 2014 or US$2.63 billion in 2014 (Yamamoto et al., 2019). State losses from the domestic commercial value of unreported timber production during 2003-2014 amount to between US$60.7 billion and US$ 81.4 billion or between US$ 5.0 billion and US$ 6.8 billion per year (KPK, 2015).

Some protected areas in Sulawesi island, the largest island in the Wallacea region, are listed as global Key Biodiversity Areas (KBA), including Panua Nature Reserve (Key Biodiversity Areas Partnership, 2020). Under Indonesian environmental legislation, the nature reserve is a protected area due to its biotic uniqueness. Yet, Panua Nature Reserve is the least benefitted protected area in the northern Sulawesi by international funding (Macdonald et al., 2011). Despite being designated as a protected area, this nature reserve has been degraded by illegal logging (Abood et al., 2015; Stibig et al., 2014), agriculture expansion, shifting cultivation, and mining industry, reflecting global and national trends of tropical forest conversion. These anthropogenic activities have fragmented a key forest corridor globally endangered Maleo bird (*Macrocephalon maleo*) from the forested habitat to its nesting ground. Unfortunately, the local authority does not have updated information on the deforestation dynamics within Panua Nature Reserve, making its protection off the priority list. Therefore, we would like to investigate the deforestation dynamics in Panua Nature Reserve and the surrounding landscape and to discuss possible solution for the land-use issue in the region.

To do so, we use Earth observation (EO) data that now standardly be used for forest monitoring because of the capability to capture earth surface widely and temporary. As one of EO satellites, Landsatrovides time-series data since 1972 and can be downloaded at no charge (US Geological Survey, 2018). Many researchers use these data for forest monitoring, especially to monitor forest degradation (Tang et al., 2010), deforestation (Higginbottom et al., 2019) and change detection (Willis, 2015). This research aims to assess deforestation in Panua Nature Reserve and surrounding landscape between 1978-2018 by using Landsat time-series images. We expected that forest gain would be lower than forest loss, similar to Indonesia's general forest change trends.

2. Methods

2.1 Study area

The study area located in Panua Nature Reserve (*Kawasan Suaka Alam*/KSA) and surrounding landscape consists of limited production forest (*Hutan Produksi Terbatas*/HPT) and convertible production forest (*Hutan Produksi yang dapat Dikonversi*/HPK) located in Pohuwato District, Gorontalo Province, Indonesia (Figure 1). These are part of Popayato-Paguat forest block and cover about 50,288 ha (502.8 square kilometres). Panua Nature Reserve is one of the key biodiversity areas (KBA) of Sulawesi (Key Biodiversity Areas Partnership, 2020) and a protected area of category Ia (UNEP-WCMC, 2021). It was established primarily to conserve nesting grounds of *Macrocephalon maleo* and to protect *Babyrousa babyrussa*, *Cynopithecus niger*, *Bubalus depressicornis*, *Macaca hecki* and some birds (Minister of Forestry, 1984).

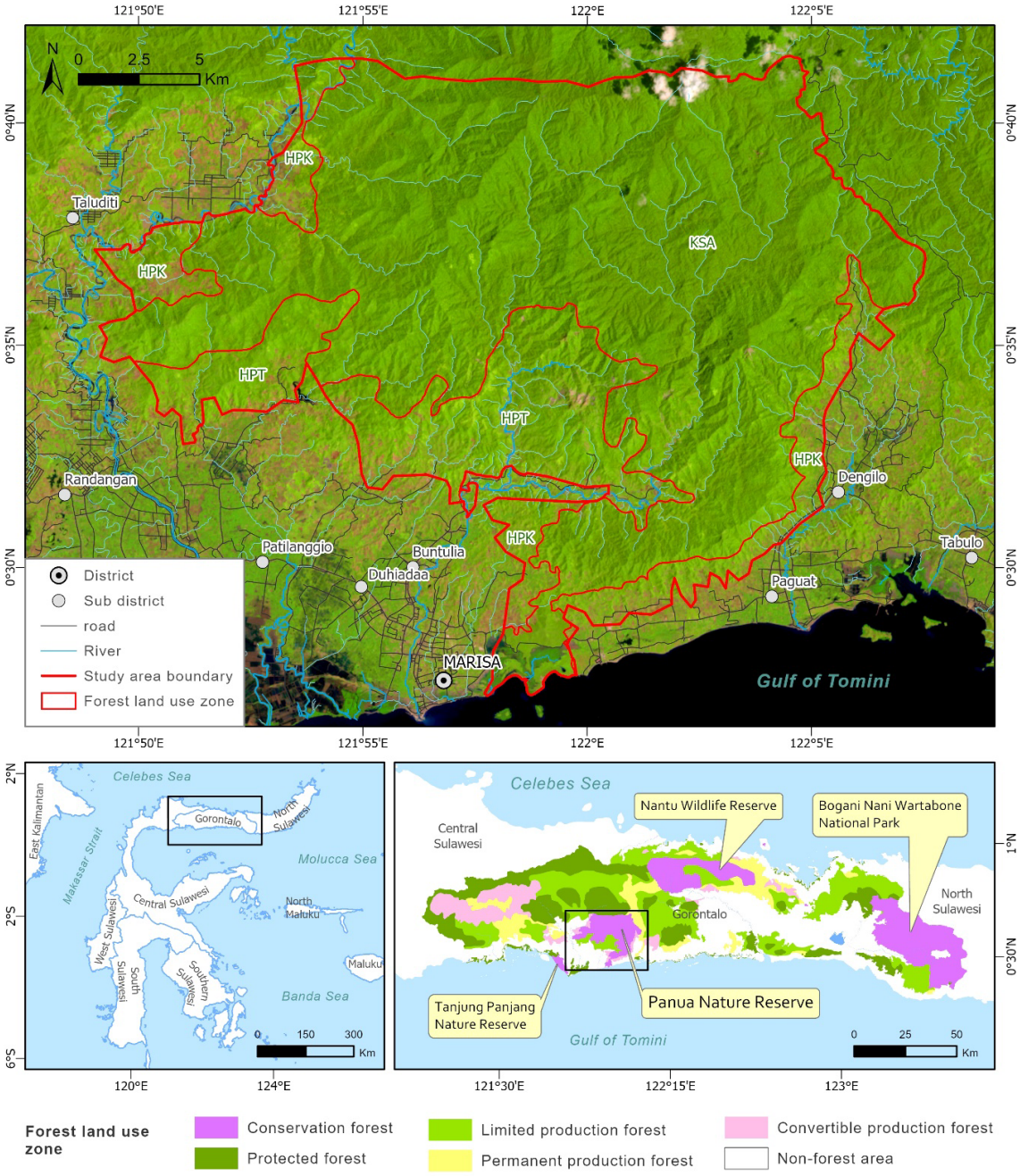


Figure 1 Study area consists of Panua Nature Reserve (KSA), limited production forest (HPT) and convertible production forest (HPK)

Table 1. A summary of forest land use zones in the study area. Forest classes, function, possible management practices and consequences of each class (Margono et al., 2012)

Forest land use	Code	Purpose/function	Possible management practices	Consequences (under sustainable forest management)
Conservation forest (including	KSA	- Designed as a forested land	- Forest usage - Forest preservation	- Dynamic forest - Stable forest without any deforestation

nature reserve)		- Preserving the biodiversity of flora fauna and their ecosystem		and forest degradation
Limited production forest	HPT	- Low-intensity logging (due to topographical condition)	- Limited logging - Very selective logging - Limited clearcutting - Post-logging silvicultural treatments	- Forest degradation
Convertible production forest	HPK	- Logging - Agriculture estate - Other uses	- Clear cutting	- Permanent and temporary deforestation - Forest degradation

More than 60% of the area is steep slopes (>30% gradient). The elevation ranges from 0 to 1,660 m asl. According to Wiriosoepartho, as cited in (Whitten et al., 1987), forest in the area can be classified into five types that are open beach forest, closed beach forest, mangrove forest, low lowland forest, and hill lowland forest. Maleo used open beach forest as nesting grounds and utilised all the forest types (except mangrove forest) as feeding place. Tropical rainforest in this area rich in biodiversity—a total of 124 bird species were recorded, including 48 Sulawesi endemics (Riley et al., 2012)—but increasingly vulnerable to deforestation and forest degradation. Therefore, spatial planning is essential to keep habitat unfragmented (Indrawan et al., 2012) or reduce the impact of the fragmentation.

2.2 Landsat data acquisition and pre-processing

Landsat data series (Path/Row: 113/60) were downloaded from the US Geological Survey for Earth Resources Observation and Science (EROS) Center via the EarthExplorer data portal (https://earthexplorer.usgs.gov/). All data were Landsat Collection 1 Level 1 products that consists of the Tier 1 (Landsat 8 Operational Land Imager/OLI and Thermal Infrared Sensor/TIRS, Landsat 5 Thematic Mapper/TM) and Tier 2 (Landsat 3 Multispectral Scanner/MSS) datasets (Table 2). Scenes in Tier 1 processed to Level 1 Precision and Terrain corrected products (L1TP) with image-to-image registration to the Global Land Survey (GLS) control of ≤12-meter Radial Root Mean Square Error (RMSE). Scenes in Tier 2 processed to L1TP with image-to-image registration to the GLS control of >12-meter RMSE. All of these have been ready for pixel-level time series analysis (USGS, 2019).

Table 2. A brief description of Landsat data uses for image classification of the study area

Landsat data series	Date acquired	Landsat collections tiers	Selected spectral bands for image classification	Spatial resolution
Landsat 3 MSS	October 14, 1978	Tier 2	B4, B5, B6, B7	60 m

Landsat 5 TM	December 17, 1996	Tier 1	B1, B2, B3, B4, B5, B7	30 m
Landsat 8 OLI/TIRS	February 13, 2018	Tier 1	B2, B3, B4, B5, B6, B7	30 m

For each scene, selected bands were combined to obtain a single layer and then clipped it according to the study area. Cloud cover was removed manually to generate cloud-free images.

2.3 Image classification

We used the Support Vector Machine (SVM) algorithm with Radial Basis Function (RBF) kernel to classify land cover from imagery. SVM is a machine learning algorithm and a supervised classifier that has been widely used in remote sensing. Some research reported that the accuracy value of the land cover map resulted from SVM is higher than the maximum likelihood classification (MLC) (Otukei & Blaschke, 2010), neural networks (NN), and classification and regression trees (CART) (Shao & Lunetta, 2012).

Our classification scheme was based on the land cover and land use classification system developed by (Anderson et al., 1976) and modified according to the features in the study area (Table 3). We chose pure pixels as training samples for each land cover class with a sample size between 25 to 400 pixels. One land cover class is a combination of five to ten training samples distributed throughout the image so that the spectral characteristics of each class represented.

Table 3. Land cover classification system

Land cover class	Description
Forest land	Lowland forest, beach forest
Wetland	Mangrove forest, non-forested wetland
Shrubland	Shrub
Agricultural land	Cropland, other agricultural lands
Barren land	Beaches, mining area, former landslide
Rural or built-up area	Settlement
Water	River, sea, lake

The performance of SVM with RBF kernel was determined by the γ parameter and the error penalty C values (Mather & Tso, 2009). The γ parameter is the width of the kernel, while the C is used to control the penalty for sample data that is not classified. For all image classification, we apply γ of 0.5 and C of 100.

2.4 Post-processing

A classification image often contains noise caused by the isolated pixels of some classes within another dominant class that forms a sizable patch (Liu & Mason, 2016). Post-classification processing is a significant step to improve the quality of the maps. It is responsible for recoding land use/cover classes, removing "salt-and-pepper" effects, and

modifying the classified image using additional data or expert knowledge (Lu et al., 2011). We used a majority filter as a post-classification processing method. This filter helps remove minority pixel classes in other pixel class groups.

2.5 Validation and accuracy assessment

Thematic information of land cover maps resulted from image classification certainly has an error classification, so its accuracy should be measured. This assessment is defined as the verification of the labelled pixel identity against the ground truth at the time of sensing at a representative sample (Gao, 2009). We collected sample units using purposive sampling methods based entirely on the operator's judgment in purposely selecting "representative" sample sites (McCoy, 2005). Limited road access and local knowledge of the study area became our consideration to choose this method.

We used the error matrix and Kappa coefficient as the tools for assessing accuracy. The former identifies overall errors for each category and misclassifications (due to confusion between categories) by category (Campbell & Wynne, 2011). An error matrix is a very effective way to represent map accuracy (Congalton & Green, 2009a) used by researchers since a long time ago.

We convert the final classification images from raster to vector to produce land cover maps of 1978, 1996, and 2018. The areas covered by the cloud were updated using the visual interpretation technique of Landsat 2 MSS imagery (acquired on December 06, 1981), Landsat 5 TM (October 17, 1997), and Landsat 8 OLI/TIRS (September 9, 2018).

2.6 Deforestation rate analysis

Post classification comparison was used to examine changes detection between two land cover maps in two intervals, 1978-1996 and 1996-2018. This approach reduces atmospheric, sensor and environmental impact, but the final accuracy depends on the classification accuracy of individual maps(Hussain et al., 2013). We then calculated the deforestation rate using the deforestation formula from The Ministry of Environment and Forestry of Indonesia (MoEF).

$$Net\ deforestation = Gross\ deforestation - reforestation$$

Gross deforestation or forest loss was defined as the sum of all area change from forest to non-forest classes. On the contrary, reforestation or forest gain was defined as the sum of all area change from non-forest into forest classes (MoEF, 2018).

Figure 2 shows the flowchart of the research method. We used the free, open-source software SAGA (System for Automated Geoscientific Analyses) version 7.5.0 (Conrad et al., 2015) to process Landsat imagery to produce landcover maps. Deforestation analysis and map visualisation were conducted in ArcGIS Pro version 2.5.0 (ESRI, 2020).

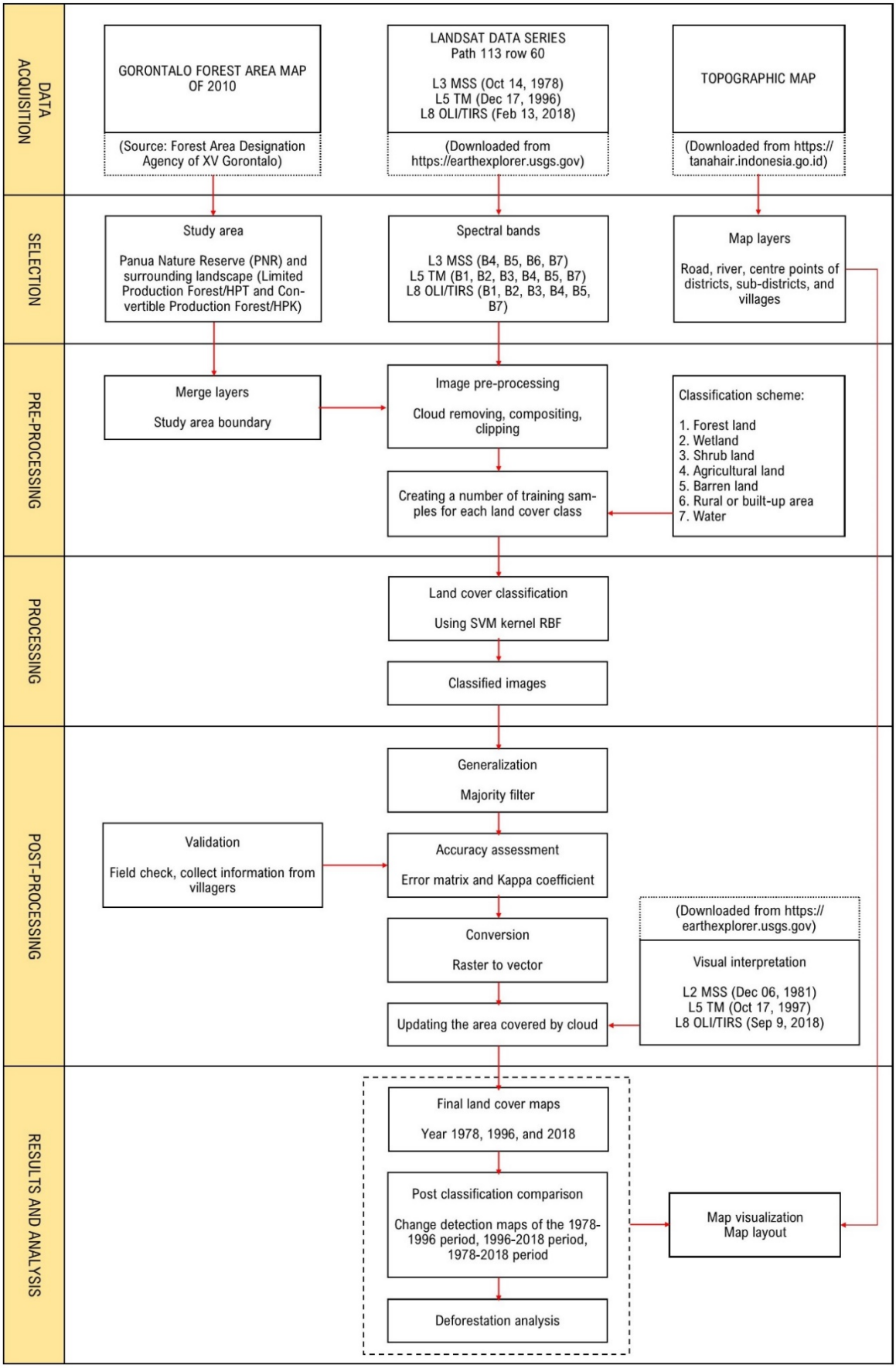


Figure 1 Research flowchart

3. Results

3.1 Land cover classification

We produced three land cover maps based on Landsat imagery (Figure 3). The land cover maps of 1978, 1996 and 2018 respectively have an overall accuracy value of 93.31% (kappa 0.91), 92.60% (kappa 0.90) and 96.05% (kappa 0.95). Based on (Congalton & Green, 2009b), the overall accuracy value that greater than 85% categorised as acceptable. These were further analysed to produce land cover change maps of the 1979-1996 and 1996-2018 periods.

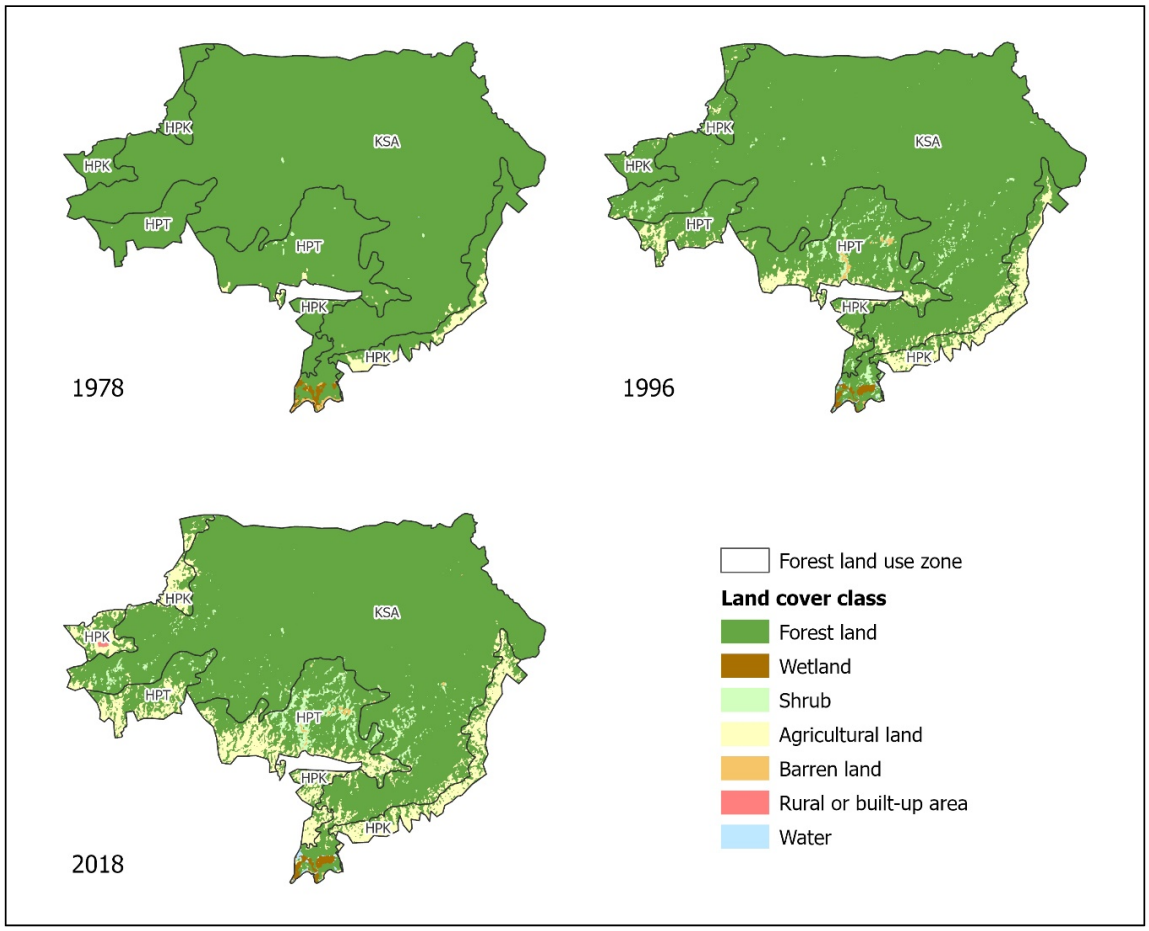


Figure 1. Land cover maps of KSA, HPT, and HPK in 1978, 1996 and 2018

3.2 Deforestation dynamic overtime

Over the past four decades, the forest cover of the study area has decreased by 6,482 hectares, approximately 13.2% of the total area. The estimation of the annual deforestation rate is 162 hectares/year. The conversion of forests to agricultural land was the main driver of deforestation. It caused forest loss up to 2,090 ha in the 1978–1996 period and 3,614 ha in the 1996–2018 period (Table 4 and Figure 4). Based on field observation, we found other drivers of deforestation, which are new rural settlements, illegal logging, gold mining, and landslides. In the 1996-2018 period, at least 30 hectares of forest land were converted into settlements. Illegal logging reduces forest density and triggers the growth of shrubs. The shrubs also grow on agricultural lands that have not cultivated for a long time. In the 1978-2018 period, the area of shrublands reached 1,656 hectares. In the same period, gold mining and landslides have slowly altered 111 hectares of forests into barren lands.

Table 4. Land cover types and deforestation in the study area from 1978 to 2018

	Area (hectares)								
		Forest change (1978 – 1996)			Forest change (1996 – 2018)			Forest change (1978 – 2018)	
Land cover types	Year 1978	Forest loss	Forest gain	Year 1996	Forest loss	Forest gain	Year 2018	Forest loss	Forest gain
Forest land	49,177	3,066		46,202	4,496		42,595	7,561	
Wetland	149	22		160	11		192	33	
Shrub land	40		3	924		293	1,309		296
Agricultural land	779		60	2,791		619	5,943		678
Barren land	108		64	115		61	92		126
Rural or built-up area							31		
Water	9		3	71		10	100		12
Total area	50,262	3,088	130	50,262	4,507	982	50,262	7,595	1,112
Net deforestation		2,958			3,524			6,482	

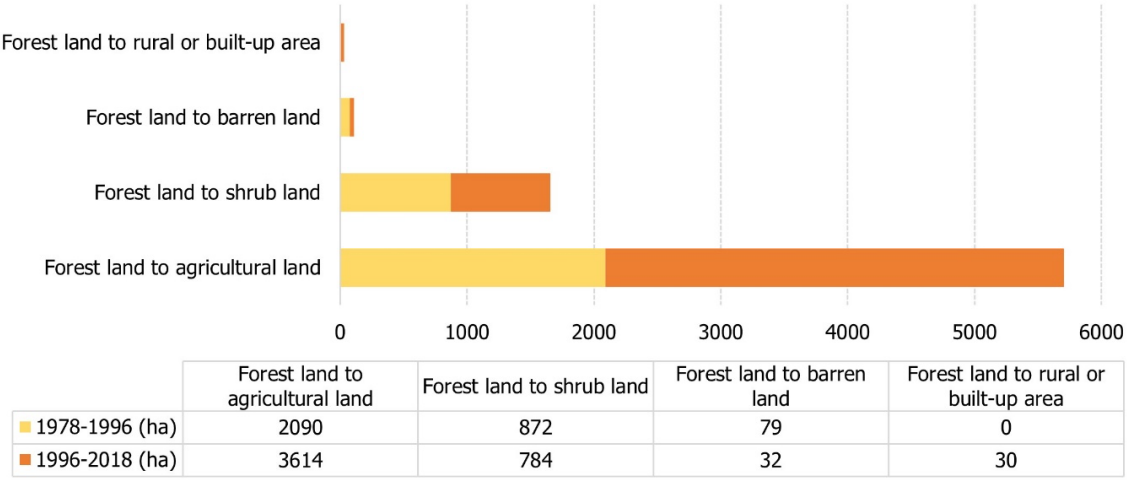


Figure 1 Forest cover change in the study area from 1978 to 2018

3.3 Deforestation over land use

The deforestation rate estimation for each forest land use zones is shown in Table 5. For four decades, the deforestation on HPT is 2,732 ha or 42.1% of the total deforested area. It is much higher than on HPK 2,566 ha or 39.6% and KSA 1,185 ha or 18.3%. The proportion of forest cover at each forest land use zones tends to decline continuously (Figure 5). Compared to 1978-1996, converted forests into agricultural lands in the 1996-2018 period increased by 217.8% on HPK, 143.1% on HPT, and 133.2% on KSA. Otherwise, in the 1996-2018 period, the barren lands dominated by gold mining on HPT and HPK decreased but increased 13 times on KSA compared to 1978-1996. In this period, the traditional gold miners cleared the forest of the KSA into new mining land because the gold reserves in HPK and HPT were running low. It also was triggered by the company that took over of potential mining area on the HPT. In the same period, about 30 hectares of HPK cleared to build two settlements.

Table 1. Land cover types and deforestation in KSA, HPT, and HPK from 1978-2018

	Areal (hectares)								
	The year 1978			Forest change 1978 – 1996					
				KSA		HPT		HPK	
Land cover types	KSA	HPT	HPK	Forest loss	Forest gain	Forest loss	Forest gain	Forest loss	Forest gain
Forest land	36,286	8,138	4,753	793		1,331		942	
Wetland	149		0.02	22				0.02	
Shrubland	13	27			2		1		
Agricultural land	31	74	675		4		5		50
Barren land	102	1	4		62		0.2		2
Rural or built-up area									
Water	9		0.2		3				0.1
Total area	36,589	8,240	5,433	816	71	1,331	7	942	52
Net deforestation				745		1,324		890	

	Areal (hectares)								
	The year 1996			Forest change (1996 – 2018)					
				KSA		HPT		HPK	
Land cover types	KSA	HPT	HPK	Forest loss	Forest gain	Forest loss	Forest gain	Forest loss	Forest gain
Forest land	35,526	6,813	3,862	839		1,692		1,965	
Wetland	159	0.5	0.2	10		0.4		0.2	
Shrub land	435	442	47		226		62		5
Agricultural land	396	890	1,505		167		168		283
Barren land	22	91	2		9		52		0.3
Rural or built-up area									
Water	51	4	16		7		2		1
Total area	36,589	8,240	5,433	849	409	1,692	284	1,965	289
Net deforestation				440		1,408		1,676	

Land cover types	Areal (hectares)								
	The year 2018			Forest change (1978 – 2018)					
				KSA		HPT		HPK	
	KSA	HPT	HPK	Forest loss	Forest gain	Forest loss	Forest gain	Forest loss	Forest gain
Forest land	35,048	5,361	2,186	1,632		3,022		2,907	
Wetland	192			33		0.4		0.2	
Shrub land	496	812	0.1		228		63		5
Agricultural land	764	1,988	3,192		172		174		333
Barren land	24	69			71		52		2
Rural or built-up area			31						
Water	65	11	24		9		2		1
Total area	36,589	8,240	5,433	1,665	480	3,023	291	2,908	341
Net deforestation				1,185		2,732		2,566	

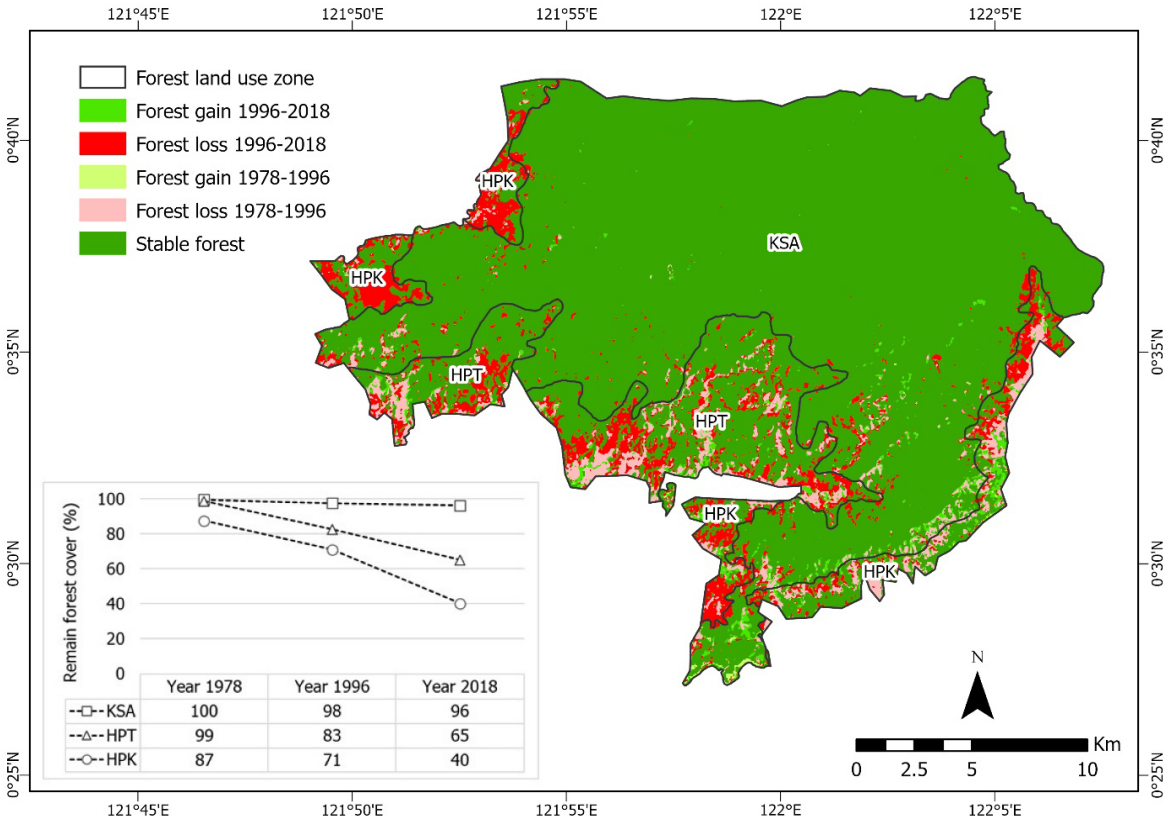


Figure 1 Deforestation in KSA, HPT, and HPK from 1978 to 2018

3.4 Limitations of research

The spatial resolution of Landsat 3 MSS is lower than Landsat 5 TM and Landsat 8 OLI/TIRS. It certainly affects the accuracy of land cover maps. The series of digital map of forest area was not completely available. So, we use the forest area map of 2010 as a baseline for the study area boundary.

4. Discussion

4.1 The government policies which potentially trigger deforestation

4.1.1 The transmigration and KAT programs

In the early 1978-1996 period, most settlements were distributed outside the forest area in Dengilo and Paguat Districts in the east and Marisa, Buntulia and Patilanggio Districts in the south. In the west and north intact and unfragmented forests remained. In the 1980s, the government placed the transmigration program in Randangan dan Taluditi Districts, both located in the west of the study area. Transmigration is the Indonesian government's program to voluntarily move people from one densely populated area to another sparsely populated place that the government has determined. Consequently, forested land was cleared gradually for transmigration sites. This program continued until the 1996-2018 period.

Another government program that places settlements around forests is the remote indigenous community (*Komunitas Adat Terpencil*/KAT) empowerment program. KAT are a group of people who are geographically isolated and socially and economically vulnerable. Since the 1990s, the settlements were built in the east, in Dengilo District. One of them was built on HPK.

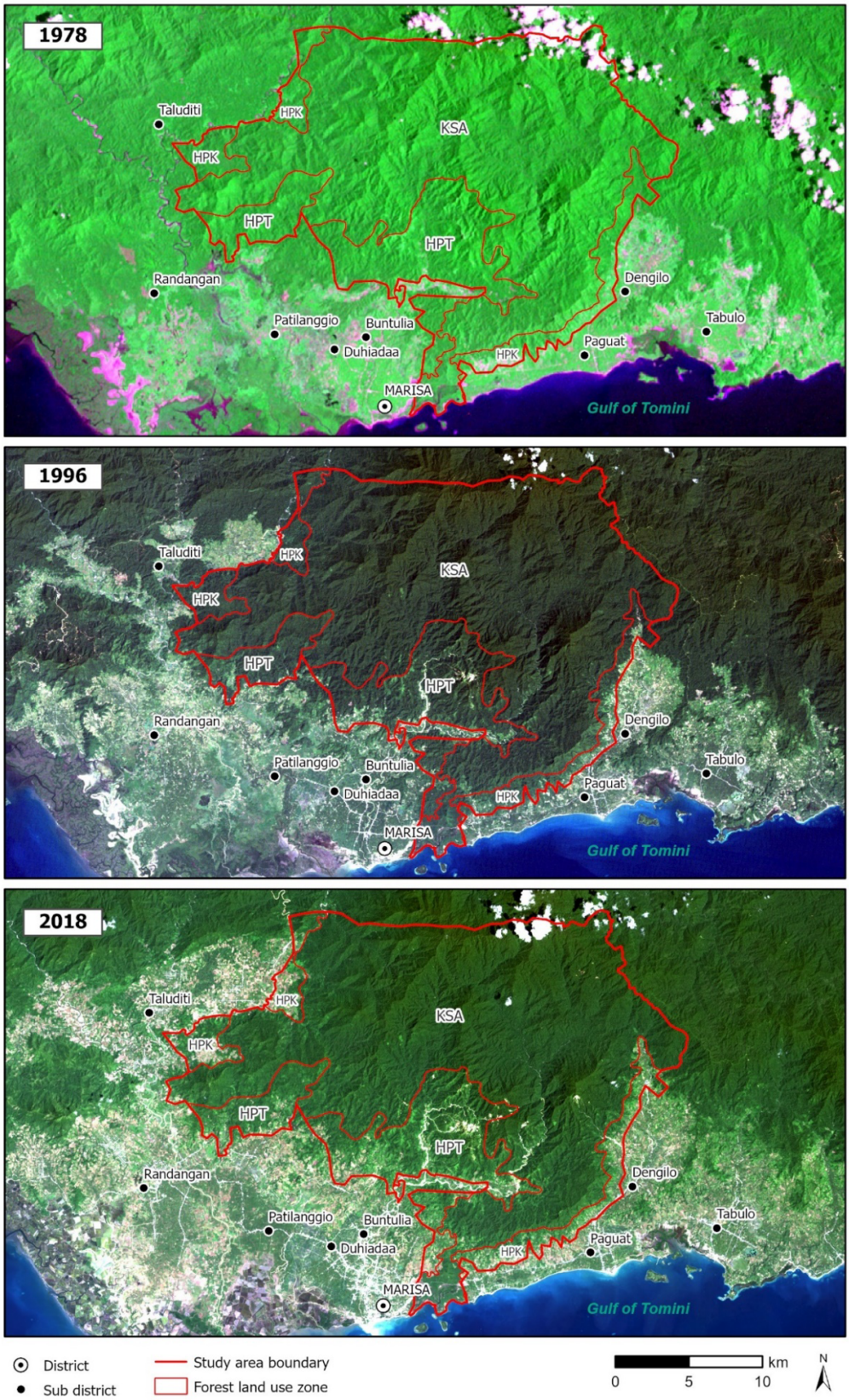


Figure 2 The visual appearance of Landsat images (natural colour) in the study area and its surroundings between 1978, 1996, and 2018

The transmigration and KAT empowerment program aims to improve the welfare and independence of the community. Each family who participates in these programs gets facilities such as a house and agricultural land that generally forested land. In many cases, they cleared more forests to expand their agricultural land. These land occupations practices have a direct influence on deforestation (Brown et al., 2016).

The placement of transmigration and KAT settlements on the forest edge has created new conservation problems. Increasing the size of the population will increase deforestation and agricultural lands (Nabil Swedan, 2020). Sometimes deforestation is an investment for farmers (Angelsen, 1999). They convert forest to agricultural land and then sell it at a low price. Population growth also increased forest degradation to supply wood demand for buildings and furniture. Illegal logging still occurs in the east, south, and west of the study area. In the north, illegal logging is very rarely found due to lack of accessibility. It is difficult to handle because the number of rangers was not proportional to the size of the work area that needs to be guarded.

4.1.2 Agricultural development through an agropolitan concept

Since the 2000s, the provincial government has implemented a corn-based agropolitan to accelerate the development of rural areas. To successfully the program, corn seeds and chemical fertilisers were distributed free of charge to farmers. The government has collaborated with investors to build a corn processing factory in Gorontalo. For nearly two decades, the program has succeeded in increasing farmers' income (Jocom et al., 2009) and made Gorontalo province of the national corn-producers(Chafid, 2016). However, government spending triggered forest conversion to agricultural land (Galinato & Galinato, 2016). It occurs both in production forests (HPT and HPK) and Panua nature reserve (KSA). We can see that the agricultural area continues to expand from 1978 to 2018 (Table 5). Statistical data also shows that the corn harvested area in several districts around the study area has increased between 2005 and 2018 (Figure 6).

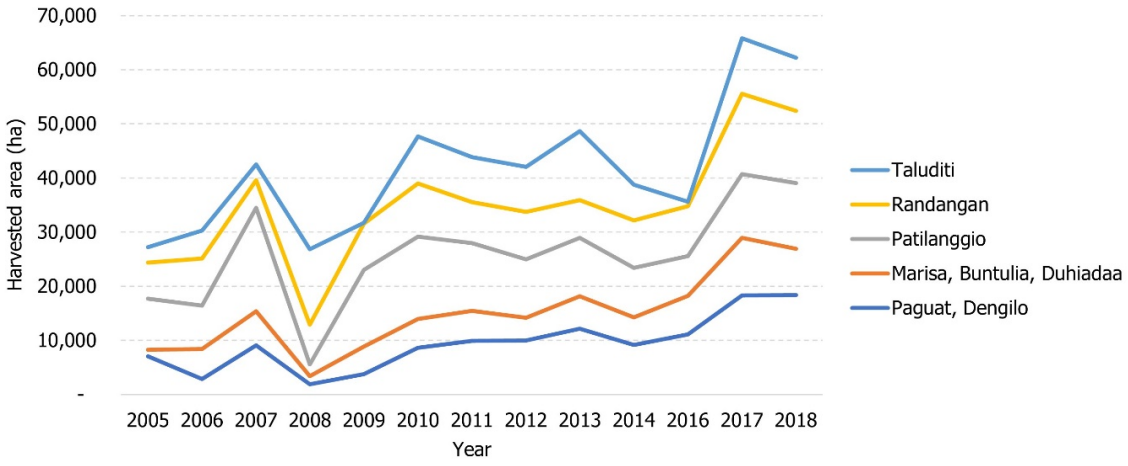


Figure 1 Corn harvested area continued to expand from 2005 to 2018. Processed from Statistics Indonesia (BPS, 2021)

Corn production is still the main achievement of the program. Without considering the land and forest sustainability, agricultural expansion contributed to releasing carbon dioxide emission per year (Pendrill et al., 2019). Unforeseen events such as erosion, floods, landslides, and habitat destruction will cause economic losses.

4.1.3 Change in the status of forest area

In 1938, the Dutch Colonial Government designated the Panua nature reserve as a natural monument with a total area of 1,500 ha. Recognising the importance of the forest as a feeding place for maleo, the Minister of Forestry (now Minister of Environment and Forestry/MoEF) of Indonesia then expanded it to 45,000 ha in 1984 and established it in 1992. Based on several considerations, some parts of Panua Nature Reserve have been altered to production forest through spatial planning of Pohuwato District in 2009. MoEF then established the Panua nature reserve with 36,575 ha in 2014 (BKSDA, 2017).

Significant changes in regulations, administrative approaches, and implementation practices enable opening the protected areas to non-forestry uses (Atmiş, 2018). Over seven decades (1938-2018), the government twice changed the Panua nature reserve boundary. The first change based on the consideration of ecological factors. But the second change seems more based on consideration of social and economic factors. Changing the nature reserve status to production forest has opened opportunities for the public and investors to access and utilise the area both for forestry and non-forestry activities such as mining. It certainly increases the threat to biodiversity. If we compare deforestation data in the first period (1978-1996) and the second period (1996-2018), altering the status of nature reserve to production forest contributes to the increasing deforestation rate.

4.2 Strategies to reduce deforestation

4.2.1 Collaborative forest monitoring

The limited number of the Natural Resources Conservation Agency (*Balai Konservasi Sumber Daya Alam*/BKSDA) officers will not prevent deforestation at any time. It is crucial to involve the local governments, Forest Management Unit (*Kesatuan Pengelola Hutan*/KPH), NGOs, police or army (Macdonald et al., 2011), and local communities (Danielsen et al., 2014) to implement forest monitoring collaboratively. A monitoring system, e.g., Spatial Monitoring and Reporting Tool (SMART), is also needed to support the implementation runs effectively and efficiently. The SMART has widely used in conservation areas in the world, including Indonesia. It is easy to use, open-source, and freely available at smartconservationtools.org. We can collect field data by using a device, stored in the computer and then spatially analysed to inform the decision-maker (Farfán et al., 2019).

4.2.2 Village land use and development plans

Generally, the villagers around the study area work as farmers. The main agricultural commodity is corn grown in monoculture on flat and sloping land. Conventional land management and long-term excessive use of chemical fertilisers and pesticides caused the soil degradation implicated in decreasing crop yields. Some farmers then decided to clear the forest into new agricultural lands. Despite obtaining fertile lands, deforestation contributes to declining soil quality (Zeraatpisheh et al., 2020).

The quality management of village natural resource needs to be improved to ensure sustainability in the future. One of the recommended approaches is village land use planning (VLUP). In this way, the villagers are involved in planning their village area. The best land uses, such as organic agriculture and agroforestry, were selected considering the existing land condition and community aspirations. The output of VLUP then can be adopted within the village regulations and village development plans. It is implementation and monitoring carried out collaboratively

The successful implementation of VLUP is expected to reduce poverty to become an effective strategy to reduce deforestation (Miyamoto, 2020). Agricultural intensification needs to be applied to minimise shifting cultivation (Jakovac et al., 2017) in the future. The implementation of VLUP also needs to use a nature-based solution approach. It could be applied in agricultural farmland both outside and inside of forest area. On the outside of the nature reserve, farmers are key players to apply sustainable agriculture. A study conducted on the neighbouring island of Borneo shows that complying with agricultural land planning into sustainable standards could break the link between agricultural expansion and environmental degradation (Smit et al., 2013).

Meanwhile, a non-sustainable approach could lead to agriculture expansion and forest degradation, so that farmers need to change their agricultural practices. Unfortunately, local farmers do not listen by instruction but by giving an example as farmer engagement through local governance is one-factor influencing farmer environmental decision making (Mills et al., 2017). Therefore, local authorities need to act as pioneers to start changing the planting pattern, and when this is successful, local farmers will follow.

Before intensifying agricultural farmland outside of the nature reserve, mapping existing agricultural farmlands that are still viable and unproductive already needs to be done. Viable farmlands are intensified through a natural approach, such as improving soil fertility by applying organic fertiliser or spreading post-harvest corn litter in the soil to attract natural decomposers. As trees planting in a variety of landscape positions and emulating the patchy distribution of forest types create diversity of habitats (Cunningham et al., 2015), planting annual fruiting tree corridors running from east to west every 50 meters could create habitat for invertebrate decomposers and pest predators as well as to reduce human-wildlife conflict. For the unproductive farmlands, indicated by the multiple crop failure events due to water shortage and pest outbreak, farmland commodity predominantly by corn production needs to be converted into other commodities. For example, fruiting trees might be more economically beneficial in drier land planting because trees could survive in more extreme condition than seasonal plants. The drier environment could even improve the sweetness level of the fruit; therefore, it could be more demanded by customers. Another strategy is by applying an agroforestry plan as the land was naturally suitable for forested ecosystems. Corn agroforestry with fruiting trees is proved to produce a more economic benefit to tropical farmers (Do et al., 2020). This plan is considered to be able to maintain forest function as well as generate local income. Cultivating diverse crops could reduce the pest attack significantly to avoid crop failure (Tscharntke et al., 2011). To fill the income gap that could not be generated before trees producing fruits, converting corn farmland into fruiting tree farm should be done part-by-part.

Inside the forested land, numerous shrub patches are formed after landslide events or after land abandonment. Being the second most dominant non-natural habitat after agricultural land, shrubland does not generate direct income and does not provide similar ecosystem functions as the forest does. Therefore, reverting shrubland into forested land could counterbalance the reforestation occurring in this landscape.

4.2.3 Social forestry

Cultivating the agricultural lands inside forest areas without a permit from the government is illegal. Ideally, the government can expel or punish the villagers, but this can lead to social conflict. The solution offered by the MoEF is social forestry issued in 2016 (MoEF, 2016).

The benefit of social forestry implementation is an economic opportunity (Rakatama & Pandit, 2020a). The villagers can propose forest management and utilisation permits collectively. The proposed priority area is production forest that has become agricultural land. Its management and utilisation refer to guidelines that the MoEF has prepared. This program expected to be successful in the future, although social and environmental issues are the main challenges of implementation (Rakatama & Pandit, 2020b).

The economic diversity of the villagers is strongly associated with increased deforestation (Dewi et al., 2005). The villagers should shift their paradigm about the forest. The economic value of forests is derived from timber and non-timber, such as freshwater, clean air, medicinal plants, ecotourism, and other non-timber forest products (NTFPs). Forests are also crucial for maintaining local temperatures cool, which is important to avoid heat-related illness (Wolff et al., 2018). Optimising the high economic value of NTFPs without destructing forest might be a solution to raise the forest economic value from the local people's perspectives. Some of the NTFPs that could be sustainably harvested are forest honey and fruits. This action plan is specifically targeted in the social forestry areas.

4.2.4 Awareness creation and capacity development

Giving the villagers awareness of biodiversity is essential for balancing their dependency on the forest and biodiversity conservation (Ali et al., 2020). The public awareness programme is expected to increase their understanding of forest resource conservation to reduce illegal activities such as illegal logging, illegal mining, converting forest to other uses, and hunting of protected animals. Villagers also need capacity building related to village land use management and entrepreneurship to open new job opportunities. Capacity building is prioritised related to agricultural and plantation products such as coconut, corn, cloves, nutmeg, etc. Together with BKSDA and KPH, the local government should facilitate the villagers to get it, supported by NGOs and companies.

The children should not imitate the behaviour of the villagers who cleared the forest. Providing access to education for children might be a comprehensive solution to create farmers who care about environmental sustainability in the future. The parents can learn from children; both parents and children will also transmit their ecological knowledge to neighbours (Vaughan et al., 2003).

5. Conclusion

Deforestation of Panua nature reserve (KSA), limited production forest (HPT), and convertible production forest (HPK) reached 6,482 hectares for the past four decades (1978-2018) or 162 ha/year. Deforestation on KSA 1,185 ha or 18.3% of the total deforested area, HPT 2,732 ha (42.1%) and HPK 2,566 ha (39.6%). The main driver of deforestation was agricultural expansion. It accounts for 86.7% of the area of deforestation. The other interrelated drivers were new rural settlements, gold mining, and illegal logging. The government policies that allegedly triggered deforestation are transmigration and KAT empowerment program, agricultural development through corn-based agropolitan, and altering the status of Panua nature reserve to production forest through spatial planning. Another driver that naturally occurred is landslides. It was found in small quantities but contributed to deforestation.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Figure a.10. Representation of one block that consists of three habitat types in proximity.



Figure a.11. Rain shelter and mesocosm set up under forest shade.



Figure a.12. Mesocosm set up (millipedes and remaining litter visible)

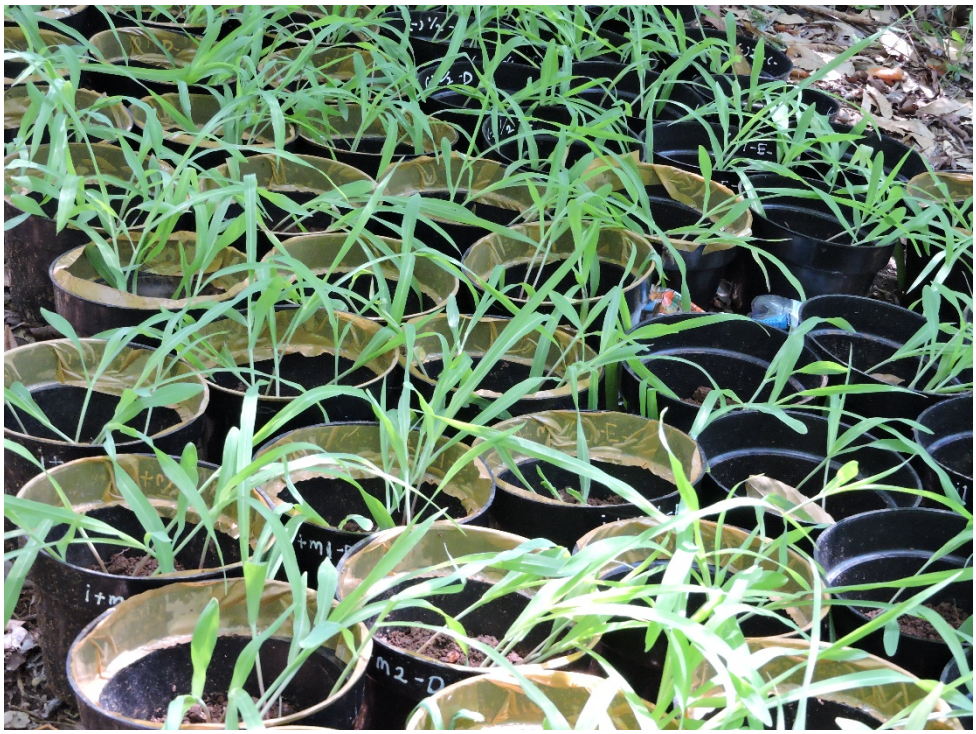


Figure a.13. Maize seedling growing from the post-mesocosm experiment soils.