Abstract
Forest conversion and fragmentation are major causes of diminished ecosystem function and biodiversity loss at a global scale. Understanding landscape effects on leaf litter decomposition and recycling of available nutrients is critical for conservation, especially in diverse tropical rainforests. Here, we studied the effects of land conversion and forest fragmentation on these two processes in a tropical ecosystem. We examined decomposition and nutrient cycling during the wet season in 22 sites across four habitat types: continuous forests, large fragmented forest patches, small fragmented forest patches, and orange plantations, in the tropical moist forest zone of NW Guanacaste, Costa Rica. The study employed a two-by-two factorial design to explore the effects of leaf litter type (site-specific litter vs. control litter) and mesh size (9 mm vs. 1 mm) on decomposition rate across land cover types. Litter bags with different mesh sizes either included (9 mm) or excluded (1 mm) macroinvertebrates. We removed litter bags from the field after 3 and 8 weeks, and cleaned and weighed the contents. Additionally, we utilized Plant Root Simulator (PRSTM) Probes to examine nutrient cycling of 10 cations and anions including N, P, K, Ca, and Mg in all site-specific litter types and both mesh treatments. We found that the rate of decomposition differed depending on habitat type, leaf litter type and mesh size. Decomposition was faster in orange plantations compared to any other forest type, and decomposition was faster in forest fragments compared to continuous forests. We determined that these differences in decomposition rates were due predominantly to differences in site-specific litter quality. Only in forest fragments did the distance to forest edge impact macroinvertebrate feeding behaviour (seen in control litter), presumably due to spatial variation in leaf litter quality. Finally, mineralization of organic nutrients differed across the four habitat types. For example, nitrogen, which is an important compound for plant cell structure and function, mineralized more quickly in orange plantations than in forest habitats. This study highlights the importance of litter quality...
differences due to fragmentation and land use in altering leaf litter decomposition and nutrient cycling.
Preface
Virginia Noble was the principal author of this research. I completed the fieldwork, data analysis and thesis preparation. However, chapter two is written as plural as it has been prepared for publication. Chapter two will be submitted for publication under co-authorship with my advisor Diane Srivastava. Diane (and my committee) provided guidance on study design, statistical analyses, thesis writing and extensive editing of the thesis.
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Dedication
Dearest Braydon Harper,

Unfortunately I never got to say goodbye and since I will never get to tell you about this latest adventure, this one’s for you. You taught us how to laugh uncontrollably, to never give up and to look at the brighter side of life. You were an amazing friend. The rainbow over Lake Nicaragua when I received the heart breaking news was a reminder of how precious memories truly are. Thank you for enriching my life and for making me a better person. Love always.
Chapter 1. General introduction

Why are forests important?
The world’s total forest area is roughly four billion hectares (FAO 2010). Even though the global deforestation rate has decreased between 2000 and 2010, from 16 million hectares/year in the 1990s to 13 million ha/year currently (area about the size of Costa Rica), deforestation remains rapid in many countries (FAO 2010). Forest ecosystems are important carbon sinks. Roughly 50 percent more carbon is stored in forest ecosystems (consisting of forest biomass, litter, deadwood and soil) than in the atmosphere (FAO 2005). Carbon is stored as lignin as well in other resistant polymeric carbon compounds within forest ecosystems (Lal 2008). Between 1990 and 2005 carbon storage by forests has decreased by 1.1 gigatonnes (FAO 2005). In fact, countries containing tropical forests are experiencing both increases in human population and development that result in more pressure on these forested ecosystems. Since the beginning of the twentieth century, roughly half of all tropical forests have been lost (Wright 2005) with the peak of the deforestation occurring in the 1980s and 1990s due mainly to conversion for agriculture (Gibbs et al. 2010).

Forest fragmentation
Fragmentation and deforestation are the most widespread disturbance to tropical forests (Whitmore 1998). Deforestation occurs when forest cover is temporarily or permanently removed for agriculture or other purposes (Grainger 1983). Forest fragmentation occurs when remaining original forest is separated into more than one patch of forest within the landscape; all else equal, the greater the number and isolation of forest patches, the more fragmented is the forest (Trzcinski et al. 1999). Forest fragmentation is generally measured by examining four effects; loss of habitat amount, the decrease in size of remaining forest patches, the increase in
the number of forest patches and the increased isolation of forest patches (Fahrig 2003). These remnant forest patches will contain a subset of the local biota (Wilcox and Murphy 1985). Species are not necessarily equally distributed among the landscape and may actually occur only in particular areas (Laurance et al. 2002). This means that species may simply be missing from fragmented areas because they never occurred there. Smaller patches will therefore often have fewer species and less habitat diversity compared to larger patches (Laurance et al. 2002). Forest structure also changes after fragmentation as forest fragments are exposed to both edge effects and area effects. Edge effects are determined by the interface between the forest ecosystem and the surrounding matrix ecosystem (Murcia 1995). Edge effects can include both abiotic and biotic changes to the forest fragment affecting the remaining species (Laurance and Yensen 1991). Only the core area of a fragment (depending on its size) will likely contain a microenvironment similar to that of the intact forest to which it once belonged (Echeverría et al. 2007). Many species are known to be sensitive to edges and require interior forest conditions (Laurance et al. 2000).

**Forest conversion**
The intensification and expansion of agriculture is one of the most significant human disturbances to the global environment (Matson et al. 1997). Conversion of tropical forests to agriculture is of particular concern because tropical forests are thought to be one of the most diverse ecosystems in the world (Whitmore 1998). The anthropogenic effects on tropical forests can be categorized as local or global effects. Local effects may include lumber and bush meat extraction, local land-cover change, and increase in invasive species (Wright 2005). Global effects include climatic and atmospheric changes (Wright 2005). Land conversion is the change of land cover type from one category to another (Meyer and Turner II 1992), for example, old
growth forest to pasture or pasture to pineapple plantation. In this thesis, I will examine some likely effects of land cover change from continuous forests to orange plantations, a dominant agricultural crop in northwestern Costa Rica.

**Matrix habitat**
Forest fragments do not occur in isolation from the altered ecosystems – the ‘matrix’ habitat – that surround them (Watling et al. 2011). The ‘matrix composition’ theoretical framework suggests that surrounding land cover types influence the abundance and number of species by affecting resource availability, colonization and dispersal mechanisms, connectivity and ultimately mortality risk (Watling et al. 2011). It is very important to consider the matrix type in conservation planning or understanding the ecology of the changing landscape. Most matrix habitats are agricultural landscapes. Previously it has been thought that landscapes can be characterized as “habitat” (where all the resources occur) and the surrounding hostile environments (Saunders et al. 1991; Fahrig 2003; Fischer and Lindenmayer 2006). However, in more recent literature a heterogeneous landscape view has been proposed to understand landscape structure (Fahrig et al. 2011). It is now apparent that species use resources from different land cover types and that the interactions within landscapes are more complex than a hostile versus habitable approach for biodiversity (Fahrig et al. 2011). Matrix habitat can influence within-fragment dynamics profoundly (Jules and Shahani 2003), but some matrix habitats support rainforest fauna better than others (Laurance et al. 2002). The more similar the matrix habitat is to the original primary forest in terms of microclimate and forest structure, the more likely that rare or sensitive species will be able to persist in the fragmented landscape (Laurance et al. 2002). Therefore, any tree-dominated matrix habitat is generally better for forest
Measuring forest fragmentation and conversion
The effects of forest fragmentation and conversion are inherently temporal processes. An example of an ideal study examining fragmentation is the Biological Dynamics of Forest Fragments Project in Manaus, Amazonas, Brazil. This study allowed for baseline data of the study area pre-fragmentation followed by studies examining the effects on this landscape post-fragmentation over time, with concurrently measured unfragmented controls (Laurance and Bierrgaard 1997; Laurance et al. 2002; Laurance et al. 2007). However, for many studies (including this one) this type of long-term study design is unfeasible and forest fragmentation and conversion have instead been examined by measuring spatial differences (a space-for-time substitution) in the landscape after landscape changes have occurred (Cascante et al. 2002; Bisong et al. 2012). In such studies the continuous forest will represent a “reference” site (landscape before fragmentation) and the fragmented forests and surrounding matrix habitat will represent the landscape following landscape change (Fahrig 2003). However, as Fahrig (2003) highlights, unlike a before and after study design, such space-for-time substitution studies have inherent limitations due to the inability to control for local site conditions, and assume that fragments are randomly located within the landscape. For example, if fragments remain forested because the soil is too thin for agriculture, there may be underlying site differences that can confound the interpretation of fragment vs. continuous differences as due to fragmentation per se.
Ecosystem function
Although forest fragmentation and conversion in tropical landscapes is a major cause of biodiversity loss (Sala et al. 2000), little is known about the consequences for ecosystem functioning (Chapin III et al. 2000). Forest conversion is likely altering the functioning of tropical ecosystems. If a forest is converted to an agricultural system without trees undoubtedly its carbon storage, nutrient cycling, and plant production will likely differ from that of forest ecosystems (Naeem et al. 1999). Habitat destruction can cause species loss, however, these losses could have a delayed impact on ecosystem functioning (Gonzalez et al. 2009). Species loss in a food web context also includes the loss of species interactions. Thus, the ecosystem effects of losing one species may not only involve the particular functions of that species, but also those of the species it interacted with (Morris 2010). However, it is possible for more than one species to have the same ecological function which provides ecological redundancy, which in turn can buffer the impact of any single species’ loss (Walker 1992). Ultimately, rates of ecosystem functions depend on the variety of interactions represented, the presence of particular key functional traits, and the abiotic environment (Scherer-Lorenzen 2005). Ecosystem functions include biogeochemical activities such as decomposition and primary production (Naeem and Wright 2003). In this thesis, I will focus on the vital biogeochemical process of leaf litter decomposition as an ecosystem function potentially affected by forest fragmentation and forest conversion in Costa Rica.

Leaf litter decomposition
The process of leaf litter decomposition is vital for site productivity and fertility (Prescott 2005b), and it is an equally important component of the global carbon budget (Aerts 1997). Decomposition transforms nearly as much carbon as photosynthesis does but occurs on or below the ground (Berg and McClaugherty 2008). The biochemistry of decomposition is multifaceted,
more so than photosynthesis (Berg and McClaugherty 2008). Put simply, leaf litter decomposition is the physical and chemical breakdown of leaf litter to its chemical components (Aerts 1997). Litter decomposition involves the mineralization and humification of lignin and cellulose by microorganisms paired simultaneously with the leaching of soluble compounds that allow for nitrogen and carbon (and other minerals) to be progressively immobilized or mineralized into the soil (Coûteaux et al. 1995). Decomposition is essential for the regeneration of organically bound nutrients (Berg and McClaugherty 2008). It is a direct determinant of the nutrient cycles of the majority of terrestrial ecosystems (Swift and Anderson 1989). Litter decomposition is controlled by both abiotic and biotic factors such as climate (micro and macro), litter quality (chemical composition) and soil organisms (marco- and micro- invertebrates) (Coûteaux et al. 1995). All or any of these three factors could be drastically altered due to forest fragmentation or forest conversion, altering the vital process of nutrient cycling. In this thesis, I assessed which of these three factors is having the greatest impact on decomposition in the study landscape.

**Decomposition at odds with carbon storage**

Any changes in decomposition rates can have widespread effects in these tropical ecosystems in terms of productivity and ecosystem functioning. During the decomposition of organic matter many essential nutrients are made available to the plants via the release of minerals (Prescott 2005a). However, another aspect of decomposition is what happens belowground in terms of humification and the accumulation of organic carbon, which could have contrasting effects on soil fertility. Increased rates of decomposition are said to be at direct odds with carbon storage, another important ecosystem function and service. Humus and soil organic matter are generally characterized as stabilized litter content that is slow decomposing due to low quality of resources
left available to detritivores (Prescott 2005a). Soil organic matter affects the soils physical and chemical properties, thus its overall “health” (Bot and Benites 2005). For example soil organic matter affects soil composition and breakdown rates, moisture holding capacity of the soil, soil organisms and their biological activity, and ultimately plant nutrient availability (Bot and Benites 2005). The soil’s ability to retain moisture, nutrients, and aeration ability directly impacts site fertility. Any increased rate in decomposition of soil organic carbon may therefore reduce the soils retention availability and overall fertility. Therefore, it is important to note that any increases in aboveground litter decomposition can directly impact the amount of litter that is left for the humification process, which is vital for long term site productivity, fertility and carbon storage.

**Santa Cecilia, Costa Rica**

The study area is located in northwestern Costa Rica in the province of Guanacaste bordered by the villages of Santa Cecilia de la Cruz and Brasilia, and part of the Área de Conservación Guanacaste (ACG) including Estación Biológica Pitilla. This part of Costa Rica has seen a drastic change in land cover type coinciding with an increase in human settlement. In the early 1990s, 8000 ha of land were purchased by Grupo de Oro S.A. (which markets under the name Del Oro) to establish a citrus industry and by the end of the 1990s over 3000 ha of this purchase had already been cultivated (Joyce 2006). In the 1990s, ACG and Del Oro had an agreement to decompose orange peels on ACG land (Janzen 2000). The project was deemed by some a huge success; not only did the orange peels decompose, they eliminated the Jaragua grass, an invasive species, within a year and a half. The decomposing peels also produced a deep black soil that allowed multi-species broadleaf herbs to grow, which served as a good substrate for forest restoration and regeneration (Janzen 2000). After this experiment Del Oro and the ACG
negotiated a contract that the organisms within the ACG would degrade 1000 truckloads a year of orange peels for 20 years (Janzen 2000). In addition, outside of the negotiated contract, the park was also naturally providing the orange plantations other environmental services such as biological control, environmental isolation and water (Janzen 2000). As payment, Del Oro would give the ACG 1200-1400 ha of forested Del Oro lands that are contiguous with the ACG forests (Janzen 1999; Janzen 2000). Unfortunately, a competitor, Ticofrut, took Del Oro to court for dumping waste in a national park and Costa Rica’s judiciary decided that the project must be terminated (Janzen 2000). This is a very interesting location where conservation meets industry. Even if only for a little time, industry and a national park had found a way to work together to promote ecosystem services, using national park area as a biodegradation site for agricultural waste which in turn promoted forest restoration (Janzen 2000).

In this thesis, I examine how the orange plantations and forest fragments isolated among the orange plantation matrix impact ecosystem functioning, particularly leaf litter decomposition and nutrient cycling.

I conducted this research using leaf litter decomposition bags. The study design is intended to disentangle three main mechanisms that impact leaf litter decomposition: microclimate, decomposer fauna and leaf litter quality. To separate the influence of these three factors, I manipulated, using a two-by-two factorial design: macroinvertebrates (excluded by small mesh or permitted access to litter) and leaf litter type (a common control species vs. site-specific litter) within litter bags, and measured decomposition rates in each of the following four habitat types. I used 6 continuous forests, 5 large forest fragments, 5 small forest fragments and 6 orange plantations in our study landscape in Costa Rica to examine leaf litter decomposition and nutrient cycling. The questions I address in this thesis are:
1. Does the rate of leaf litter decomposition differ between orange plantations and forested habitat?

2. Does the rate of leaf litter decomposition differ between forest fragments and continuous forests?

3. Does the size of forest fragments influence the rate of leaf litter decomposition?

4. Are the observed effects of forest conversion and forest fragmentation on decomposition primarily due to differences in litter quality, macroinvertebrate communities, or microclimate?

5. What are the observed effects of forest conversion and fragmentation on the availability of mineral nutrients?
Chapter 2. The effects of tropical forest fragmentation and land use on leaf litter decomposition and nutrient cycling

Introduction
Large scale forest fragmentation and conversion is a dominant feature of today’s tropical landscapes. Much of this forest loss is linked to the intensification of agriculture (Matson et al. 1997; Steffan-Dewenter et al. 2007; Gibbs et al. 2010). In the tropics as a whole, in the 1980s and 1990s, conversion of disturbed or intact forests accounted for 80% of new agricultural land (Gibbs et al. 2010). Although forest fragmentation and conversion in these tropical landscapes is a major cause of biodiversity loss (Sala et al. 2000), little is known about the consequences for ecosystem functioning (Chapin III et al. 2000). In tropical forests, one of the most important ecosystem functions is the terrestrial decomposition of plant litter, resulting in the transfer of aboveground nutrients fixed in plant biomass to belowground nutrient pools in the soil (Aber and Melillo 1991). Such nutrient recycling fuels plant growth on the ancient, nutrient-poor soils that underlie many tropical forests (Vitousek and Sanford Jr. 1986), and therefore can potentially drive effects of landscape change on primary productivity, carbon fixation and biodiversity.

Forest fragmentation and conversion could affect litter decomposition through changing any of the three dominant determinants of decomposition rates: litter quality, the decomposer community, or environmental microclimate (Meentemeyer 1978; Gonzalez and Seastedt 2001; Powers et al. 2009). Of these, litter quality arguably has the greatest effect (Meentemeyer 1978; Cotrufo et al. 1998; Hättenschwiler et al. 2005), for example resulting in greater variance in decomposition between plant species within a site than between different climatic zones (Cornwell et al. 2008). In general, higher decomposition rates are associated with detrital characteristics such as high nutrient content, low levels of secondary compounds and low amounts of structural compounds such as lignin and fibre (Hättenschwiler et al. 2011).
Forest fragmentation can result in shifts in the tree species composition that are associated with certain leaf traits. Small fragments often experience elevated rates of disturbance – such as wind throw (Laurance 1997) – that permeate deep into the fragment (Laurance et al. 2002). Such disturbance regimes lead to the dominance of pioneer species of trees; that is, trees that allocate resources to growth rather than defenses, and thus typically have leaves with lower toughness, phenols and fibers that otherwise would defend the plant, and higher nitrogen and water content for rapid growth (Coley 1983). By contrast, old growth species tend to be slower growing, due to limited habitat resources, and invest more in defences such as phenols and lignin content and are less nutritious and less palatable for macroinvertebrates (Coley et al. 1985; Coley 1988). By and large, these traits of living leaves are correlated with similar traits of detrital leaves (Wright et al. 2004). Thus, leaf litter from pioneer species has been found to decompose faster than that of later successional species (Kazakou et al. 2006). We would therefore expect forest fragmentation to accelerate the decomposition of leaf litter because of a shift in leaf traits.

Forest conversion to agriculture may have even more extreme effects on detrital quality. Agricultural species are almost always of different leaf quality from the original forest, and often consist of species selected to have the rapid growth rates that optimize biomass production. Agricultural species can cause large shifts in plant community structure and plant functional diversity that alter leaf litter decomposition (Fortunel et al. 2009). For example, coffee leaves decompose much faster than those of shade trees in the same plantation (Aranguren and Herrera 1983). The litter produced by agricultural species may have different nutrient levels compared to the original forest leaves, either due to different nutrient requirements (Palma et al. 2000) or rates of nutrient reabsorption (Aerts and Chapin 2000), as well as changes in nutrient availability due to agricultural practices (e.g. irrigation, fertilization, tilling and application of herbicides).
In addition to leaf quality, the structure of the decomposer community can also influence detrital decomposition rates (Gonzalez and Seastedt 2001). The decomposer community consists of micro-organisms (bacteria, fungi), which are able to chemically break down organic compounds, as well as micro-invertebrates (mites, collembolans) and macro-invertebrates (e.g. insects, isopods, annelids). Macroinvertebrates are particularly important in facilitating litter decomposition, either by direct ingestion, which brings the detritus in contact with their gut-dwelling microbes (Collins 1981; Lavelle et al. 1993), by increasing the availability or quality of litter to microbes (Swift et al. 1979; Lavelle et al. 1997; Belovsky and Slade 2000) or by promoting microbial growth via habitat modification or grazing (Seastedt and Crossley 1980; Lavelle 1997). As a consequence, changes in macroinvertebrate community structure can have strong impacts on decomposition rates (Gonzalez and Seastedt 2001).

Both forest fragmentation and forest conversion are known to influence litter macro-invertebrate communities. However, these landscape changes can result in habitat that is less suitable for some macro-invertebrates, but more suitable for others, and the net effect of these changes will depend on the particular traits and abundances of the species involved (Ries and Sisk 2008). For example, although forest fragmentation is linked to reductions in some groups of macro-invertebrates (e.g. dung beetles: Chapman et al. 2003; leaf litter beetles: Didham et al. 1998; Termites: DeSouza and Brown 1994), it also benefits other groups (e.g. butterflies: Brown and Hutchings 1997; litter-feeding termites: DeSouza and Brown 1994), and so can results in changes in macroinvertebrate composition even in the absence of a similar shift in species richness (e.g. carabid beetles: Davies and Margules 1998). The impacts of forest conversion to agriculture also depend strongly on the type of agriculture. For example, in the Azores, conversion of native forests to highly modified intensive pasture resulted in the replacement of
native by introduced arthropods, whereas conversion to an unmanaged exotic forest retained suitable habitat for some native species, such as saproxylic beetles (Meijer et al. 2011). Similarly, the composition of leaf litter ants is preserved in cacao plantations following conversion from primary forests (Belshaw and Bolton 1993). The intensification of agricultural practices, such as soil tilling, can have large direct impacts on soil macroinvertebrates (Giller et al. 1997). Other agricultural practices, such as the use of herbicides and cultivation, have unpredictable and nonlinear effects on soil faunal diversity (Wardle 1995).

Finally, decomposition rates are also influenced by aspects of the macro- and microclimate, such as temperature and humidity. In general, decomposition rates are greater under warm, moist conditions (Powers et al. 2009; Aerts 1997; Salinas et al. 2011). Soil pH (Cunningham 1963) and litter depth also influence decomposition in the tropics. Soil formation and nutrient cycling are also impacted by macro- and micro-climate (Lavelle et al. 1993) which directly affect litter quality (Swift and Anderson 1989). Again, both forest fragmentation and conversion often result in substantial changes in the microclimate. Compared with forest interiors, forest edges often exhibit reduced air and soil moisture, increased understory air temperatures (Williams-Linera 1990; Kapos et al. 1997), and – due to canopy gaps caused by windthrow – increased penetration of rain and solar radiation (Saunders et al. 1991). Such edge effects on microclimate can permeate long distances (200m to 500m from forest edge (Laurance 1991)), even to the center of 1 ha fragments.

The ground-level microclimate in dense continuous rainforest differs significantly from the canopy (Geiger et al. 2009). Dense forest cover reduces incoming and outgoing solar radiation (Geiger et al. 2009). Forest canopies also protect the forest floor from direct contact with rain, but the cooler, darker micro-environment can permit soils to be continuously moist
Land conversion and forest clearing lead to higher net solar radiation penetration by day and increased outgoing radiation by night, leading to higher and more variable daily temperatures (Rosenberg 1974), and loss of soil moisture (Ghuman and Lal 1987). In summary, although the warmer temperatures during the day associated with both forest fragmentation and conversion should increase decomposition rates, this may be offset by reductions in soil moisture and lower temperatures at night associated with reduced decomposition.

In this study, we examine the effects of forest fragmentation and conversion on litter decomposition and soil nutrient availability and determine the degree to which the above three mechanisms (i.e. changes in litter quality, macro-invertebrates, or micro-climate) is responsible for these effects. Our study is centered in northwestern Costa Rica. Primary forest cover in Costa Rica declined from 67% the 1940s to 17% by 1983 (Sader and Joyce 1988). By 1991 the total closed forest cover (i.e. primary and secondary forest combined) was only 29% (Sánchez-Azofeifa et al. 2001), increasing slightly (1.6%) in the following two decades due to an increase in the area of protected forests (FAO 2010). Currently, 25% of Costa Rica’s land is protected under Sistema Nacional de Areas de Conservacion (Janzen 2000). Costa Rica’s seasonally moist forest ecotone has only about 10% of its original forest cover remaining after the last 100 years and what remains is generally remaining in forest fragments (WWF 2006). The protected areas in this ecotone only contain about 30 000 ha of forest (WWF 2006). The landscape surrounding protected forested areas have been accompanied by an increase in forest fragmentation. It has been argued that these remnant forests can still contribute substantially to biodiversity conservation (Daily et al. 2001), but their value in preserving ecosystem functioning has yet to be evaluated. Much of the forest loss in Costa Rica is attributed to conversion to agriculture,
primarily cattle (dating back to the 1950s), bananas, coffee, pineapple, oranges and oil palms. We focus on forest conversion to orange plantations, the dominant crop in our study area. The five main questions that this study addresses are:

1. Does the rate of leaf litter decomposition differ between orange plantations and forested habitat?
2. Does the rate of leaf litter decomposition differ between forest fragments and continuous forests?
3. Does the size of forest fragments influence the rate of leaf litter decomposition?
4. Are the observed effects of forest conversion and forest fragmentation on decomposition primarily due to differences in litter quality, macroinvertebrate communities, or microclimate?
5. What are the observed effects of forest conversion and fragmentation on the availability of mineral nutrients?

Methods

Study area description
This study was based on an 11 x 11 km landscape in northwestern Costa Rica, bordered by the villages of Santa Cecilia de la Cruz and Brasilia, and part of the Área de Conservación Guanacaste (ACG) including Estación Biológica Pitilla. This area has a distinct dry season from January through May and ranges from 300-500 m above sea level. This part of Costa Rica has seen a drastic change in land cover type coinciding with an increase in human settlement. In the early 1990s, 8000 ha of land were purchased by Grupo de Oro S.A. (which markets under the name Del Oro) to establish a citrus industry and by the end of the 1990s over 3000 ha of this purchase had already been planted (Joyce 2006). Orange plantations have been a dominant land-use cover type in the area of Santa Cecilia over the last 20 years. Other land cover types are
secondary forest of varying successional stages, pasture, pineapple fields and other local crops (e.g., beans and bananas). In the process of forest conversion to agriculture, forest patches of varying sizes remain in the agricultural matrix.

**Site selection**
We were interested in two main forest disturbances that may affect leaf litter decomposition (forest conversion, forest fragmentation) and within forest fragmentation we were interested in the effects of fragment size. To examine if landscape differences had an effect on leaf litter decomposition we selected sites that included protected continuous rainforest, fragmented forest patches within the dominant matrix of orange plantations and orange plantations themselves. Within this study area, 6 protected continuous forests, 6 orange plantations and 10 forest patches were selected to examine whether the rate of leaf litter decomposition differences after forest conversion (i.e. comparison of forests with orange plantations) or forest fragmentation (i.e. comparison of continuous forest with fragmented forest), or with fragment size (i.e. large fragments vs. small fragments) (Fig. 2.1-2.4). We selected the sites carefully to ensure that there was no correlation between habitats and any of elevation (ANOVA: $F_3 =0.29, p=0.83$), latitude (ANOVA: $F_3=0.70, p=0.56$), or longitude (ANOVA: $F_3=0.84, p=0.49$). To be clear, our measurements of forest conversion and fragmentation effects are not measured over time, as in a complete before and after deforestation measurement. Here we approximate deforestation as a spatial process at one single point in time. In this study, our understanding of the effects of forest fragmentation is based on the spatial comparison of continuous forests (“reference sites”) to forest fragments (“post-fragmentation”). We also examined the effects of forest conversion by pooling continuous forests and forest fragments which allows for a spatial comparison of forested habitat (“forests”) to orange plantations (“post-conversion”). Therefore, the differences between these habitat type comparisons can help us predict the effects of forest conversion and
forest fragmentation in this landscape. However, a study design that looks at forest conversion and forest fragmentation with this space-for-time substitution has inherent limitations compared to studies able to examine these landscape changes in both time and space (see “Limitations”). The orange plantations included four plantation sites in the non-organic sector of Del Oro and two smaller privately owned orange plantations, which also used agrochemicals. The 10 forest patches were located within the matrix of orange plantations, with the exception of two fragments surrounded by old pasture (SA, LA). Forest patches were selected and divided into two size categories; large (n=5; 6.48-41.59 ha) and small (n=5; 1.32-8.73 ha) fragments and size categories were based on the width of the geometric center of the forest fragment, to examine if the size of the remaining patches affected decomposition rates. The study took place from July to September 2011, in the early wet season.

Mechanisms
Any differences in leaf litter decomposition between habitat types could be due to differential impacts of macroinvertebrates, site-specific leaf litter or other habitat differences such as microclimate (Fig. 2.5). To separate the influence of these three factors, we manipulated, using a two-by-two factorial design, macroinvertebrates (excluded by small mesh or permitted access to litter) and leaf litter type (a common control species vs. site-specific litter) within litter bags, and measured decomposition rates in each of the four habitat types (continuous forest, large forest fragment, small forest fragment, orange plantation). If leaf quality differences between habitats drove decomposition differences, we would expect only the litter bags with site-specific litter to show a significant effect of habitat (Fig. 2.6a). Similarly, if habitat effects on macroinvertebrates influenced decomposition, we would expect only the litter bags that permitted macroinvertebrate access to show significant habitat effects (Fig. 2.6b). Any differences between habitats in litter decomposition that persisted despite macroinvertebrate exclusion and a common litter species
would appear to be due to habitat differences other than leaf quality or macroinvertebrate activity, most likely differences in microclimate between habitat types (but possibly also differences in the microbial or microinvertebrate community) (Vasconcelos and Laurance 2005; Fig. 2.6c).

**Litter bag placement**
To examine leaf litter decomposition in each of the 22 sites we first established transects using a GPS and a compass. The transects in the fragmented forest patches (both small and large) began at the edge of the widest part of the patch and continued to the middle of the patch, thus larger patches had longer transects. This design ensured that both edge and centre habitat of all fragments were included in our survey. If we had instead used a fixed-length transect, we would have sampled primarily edge habitat in large fragments, biasing our results. The transects in the continuous forests started 200 m in from the edge and proceeded 150 m into the forest, perpendicular to the edge. We wanted to ensure that continuous forest transects were free from edge effects, and previous studies have found edge effects generally do not permeate more than 200 m into continuous forest (Didham 1998). Continuous forest transects were 150 m long to match the average transect length in the fragmented patches. In orange plantations 150 m transects were also used, starting at the plantation edges of the orange plantations and proceeding inwards.

Each transect was divided into five equally-sized segments, and a 4m² plot randomly located on each segment, ensuring that decomposition plots represented the habitat along the entire transect even though transects may be of different length (Fig. 2.7). This allowed us to conclude that results are based on land-use change effects to the forest and not confounded by spurious correlations between plot placements and distance to forest edge. Each decomposition
plot was located 10 m from the transect, with the cardinal direction randomized. In each decomposition plot we placed eight litter bags, consisting of two replicates of all combinations of mesh size (1 mm, 9 mm) and litter type (control, site-specific), during the period July 8-16, 2011. One replicate was harvested in each of two sampling periods, as described shortly. Each litter bag was placed on a separate 20 x 20 cm area that had been cleared of litter within the decomposition plot so that the litter bags were in direct contact with the soil, but surrounding litter was not disturbed.

**Litter bag construction and harvest**

Litter bags (20 x 20 cm) were constructed from mesh of either 9 mm or 1 mm size that permitted (9 mm) or excluded (1 mm) macroinvertebrates. The leaf litter type was either control litter or site-specific litter (Fig. 2.8). Control leaf litter was *Conostegia xalapensis*, a short tree common in pastures and secondary forest, whose senescent leaves were hand-collected from pastures close to Estación Biológica Pitilla. Site-specific leaf litter was collected from two 1m² areas of the forest floor; 1m² from the center of the transect (5 m from the transect) and a sample from the edge was taken at the beginning of the transects (5 m from the transect) to provide a representation of the mixture of leaf litter within each site (edge and interior litter) without disturbing the plots themselves.

Both leaf litter types were first filtered through a 9 mm mesh to ensure that leaves placed in the litter bags would not immediately fall through the mesh. Leaves selected for the study were dried in a conventional oven at 60°C to a constant dry mass of 5.1 grams. The brittle, dry leaves were subsequently moistened for at least 12 hours before the litter bags were transported to sites to avoid fracturing of leaves during transport. Litter bags were also transported to the
study sites within plastic bags to minimize loss of leaves during transportation (loss during transport was small and not detectible (< 0.1g), as our scales smallest measurement was 0.1g).

Three weeks into the experiment, one of each type of litter bag in each plot was chosen at random for removal. The remaining four litter bags remained at the plot until the end of the 8 week period when they were also removed. Litter bags were immediately placed in plastic bags and brought back to the field station. The leaves in each litter bag were removed and cleaned carefully, using paintbrushes, water and paper towel in sorting trays, to prevent the loss of loose leaf fragments. The litter samples were then dried and weighed; final dry mass was recorded to the nearest 0.1g.

**Nutrients**

Plant Root Simulator (PRSTM™; Western Ag. Innovations, Saskatoon, SK, Canada) probes were used to examine the consequences of forest conversion and fragmentation on mineral nutrient availability, and to isolate the effect of macroinvertebrates on mineral nutrient availability. The PRSTM™ probes function by absorbing available nutrients from the soil, analogous to absorption by a plant root. PRSTM™ probes were placed under all site-specific litter types for both mesh size treatments and measured the nutrient availability of macronutrients (nitrogen, phosphorus, magnesium, potassium, calcium and sulphur) and micronutrients (manganese, copper, iron and zinc). Although boron, aluminum, lead and cadmium were also assayed, the concentrations of these elements were below detection limits, so they are not considered further. Financial constraints prevented us from placing PRSTM™ probes under control litter bags as well. At each of the 22 sampling sites, four of the five plots along the transect line were randomly selected to have a pair of PRS™ probes (one cation and one anion probe). The PRS™ probes were positioned during week 4 of the study under the remaining site-specific litter bags (both 1 mm
and 9mm mesh). The probes were placed into the soil directly under the litter bags at a 45-degree angle using a rubber mallet. After three weeks the PRST™ probes were removed from the soil and immediately washed of all soil, using deionized water. The probes were then refrigerated until being shipped to Western Ag. Innovations (Saskatoon, Canada) for analysis. Upon analysis, data from PRST™ probes from a particular litterbag type within a site were pooled. The PRST™ probes allowed us to examine if the nutrients varied between forest types and further investigate the role of macroinvertebrates in the cycling of available nutrients during the decomposition process.

Site characteristics
We characterized the microclimate of each site by relative humidity and temperature, measured every 30 minutes with a LogTag™ Datalogger (MicroDAQ.com) placed at the center of each fragment or 150 m in from a distinct edge in orange plantations or 350 m from a forest edge in continuous forests on a tree at breast height for the duration of the study. Litter fall was also quantified in each plot location within each site using litter fall traps consisting of 1m² of 2.5 cm diameter mesh hung at approximately 1.4 m from the ground, 5 m from the transect, for the 8 weeks of the study. The P content of leaf litter from the four forest types was determined using a persulfate digestion method and an ascorbic acid method (APHA 1992). Dried leaf material was ground in a ball mill prior to measuring the mass of a homogenized subsample on a digital microbalance (±0.1 μg).

Data analysis
We first determined decomposition rates for litter in each litter bag type in each decomposition plot at each site. Each decomposition rate was estimated as the exponent in an exponential decay model of leaf litter mass over time, with the intercept fixed as the initial litter mass. Thus each decomposition rate was based on three measurements: initial litter mass, mass after three weeks, and mass after eight weeks. Exponential decay models are commonly used to understand the
litter decomposition process (Jenny et al. 1949; Olson 1963), and it is often recommended to fix the intercept at the initial mass as there is no decomposition by definition at time zero (Wieder and Lang 1982). In a few cases, litter mass was higher after eight weeks than three weeks, probably due to heterogeneity between replicates within decomposition plots. In this case, we estimated two decay constants, one based on the initial and three week mass, and one based on the initial and eight week mass and averaged these two estimates.

Linear mixed effects models (using the nlme package in R; Pinheiro et al. 2012) were then used to model (“full model”) litter decomposition rate as a function of habitat types (4 levels), two litter bag mesh sizes and two litter types and all interactions of these three fixed factors, with site identity as a random factor.

We had two goals for our analysis. First, we sought to compare particular types of habitat to compare the effects of forest conversion with forest fragmentation. Second, we sought to examine patterns in particular litter bags to test particular mechanisms for habitat differences. We used model simplification and model comparison to meet these goals (see below).

To determine whether ‘forest conversion’ was an important predictor we simplified the model by pooling all the fragments and continuous forest as one habitat type (pooled forest) and compared this to the orange plantations (converted forest). We then compared (using ANOVA with likelihood ratios) this simplified model (model 1) with a model of decomposition rates without any habitat factors to determine whether ‘forest conversion’ significantly affected decomposition. To investigate whether ‘forest fragmentation’ had an effect on leaf litter decomposition we examined, using ANOVA, the effect of dividing the “pooled forest” category in model 1 into “continuous forest” and “fragmented forest” (i.e. both small and large fragments) (model 2); a significant difference between model 1 and 2 indicated changes in decomposition
between continuous forest and fragments. Finally, to determine whether fragment size affected leaf litter decomposition rates we compared model 2 and the full model; a significant difference indicated that large and small fragments differed in their decomposition rates.

After using model comparisons to determine the impact of ‘forest conversion’, ‘fragmentation’ and fragment size on litter decomposition in general, we used contrasts to determine which types of litter bags were responsible for any significant effects (using contrast package within R; Kuhn et al. 2011). Our proposed mechanisms can be distinguished by the results obtained from our litter bag treatments (see “Mechanisms” and Fig. 2.6).

Finally we sought to test if, within the fragments, either distance to forest edge or continuous measures of fragment area influenced leaf litter decomposition in our linear mixed effects models. Note that distance to edge and fragment area show some covariance ($r=0.73$, $p=0.017$), as the centers of larger patches are necessarily further from the edge. Our fragment model was a mixed linear effect model with distance to forest edge, fragment area, litter type and mesh type as fixed factors, and fragment identity as a random factor. All interactions between fixed factors were included, save the interaction between distance to edge and area because of the covariance ($r=0.73$, $p=0.017$). We then explored, using ANOVA, whether either distance to edge or area could be dropped from this model.

We also examined the effects of forest conversion and fragmentation on nutrient cycling by using the same model comparisons as for decomposition rates, but omitting the litter type factor (nutrients were only assessed under site-specific litter). Because the availability of multiple nutrients was assessed by each PRST™ probe, we were concerned about non-independence between multiple correlated response variables. Therefore, we first assessed overall effects of habitat and macroinvertebrates on the 10 macro- and micronutrients using a
multivariate permutation analysis (PERMANOVA, using the package vegan within R; Oksanen et al. 2011). Following significant overall effects due to habitat and/or macroinvertebrates in the PERMANOVA analysis, we used individual ANOVAs to determine which nutrients responded most to treatments. Data for several of the nutrients had to be log10 transformed (P, K, S, Mn, Cu, Zn) to conform to assumptions of normality and homoscedasticity. All analyses were completed in R 2.12.1. (http://www.R-project.org).

Results

Litter quality and quantity
Litter fall differed in quality, as approximated by phosphorus concentration (phosphorus is a limiting nutrient in most tropical terrestrial ecosystems). The highest phosphorus concentrations were found in orange litter (orange vs. other litter: L ratio = 14.5, p = 0.0001). Native trees tended to increase in phosphorus concentration along a disturbance gradient (0.04% ± 0.01 < 0.05% ± 0.02 < 0.06% ± 0.02 < 0.08%), from continuous forest to large fragments to small fragments to pasture (control litter) (Fig. 2.9). Although fragmentation and fragment size effects were not significant (L ratio = 2.83, 1.81; p = 0.09, 0.17 respectively), litter fall differed across habitat types in our study area (F_{3,18}=22.59, p<0.0001). Litter fall was greater in forest fragments, as compared to continuous forests (L ratio=6.37, p=0.012) but there was no difference between our forest fragment patch sizes (L ratio=0.003, p=0.957). Litter fall in orange plantations was significantly lower compared to that of pooled forested habitat (L ratio=26.66, p<0.0001).

Microclimate
Landscape differences had profound effects on the microclimate of sites, in terms of both temperature and humidity. Orange plantations, as compared to pooled forested habitat, resulted generally in hotter, drier and more temporally variable microclimates. Specifically, using a model
simplification procedure (see “Methods”), we found that ‘forest conversion’ (orange plantations versus pooled forests) increased daily mean (Likelihood ratio=17.4, p<0.0001), maximum (L ratio=26.8, p<0.0001), and daily range in temperature (L ratio = 30.1, p<0.0001) but did not impact daily minimum temperature (L ratio=0.68, p=0.41; Fig. 2.10). Orange plantations, as compared to pooled forests, also had a lower daily mean (L ratio = 13.2, p=0.0003) and minimum humidity (L ratio = 14.6, p=0.0001), and a greater daily range in humidity (L ratio =14.6, p =0.0001), but no difference in maximum humidity (L ratio=2.97, p=0.085). Forest fragments, as compared to continuous forests, showed a greater range of daily temperature (L ratio=3.92, p=0.0476) and marginally higher maximum temperatures (L ratio=3.27, p=0.0705) but no difference in humidity (see “Appendix”). However, fragment size affected humidity but not temperature. Large fragments as compared to small fragments had higher daily average (L ratio =6.69, p=0.0097) and minimum (L ratio=9.20, p=0.0024) humidity. Small fragments had a greater fluctuation in range of daily humidity (L ratio=7.92, p=0.0049).

Decomposition
Leaf litter decomposition was affected by habitat type (linear mixed effect model, F₃,₁₈=18.9, p<0.0001) and was greater when litter bags allowed macroinvertebrate access (F₁,₄₀₆=164, p<0.0001), although these two factors did not operate independently (habitat type x macroinvertebrate F₃,₄₀₆=8.59, p<0.0001). Leaf litter type (control vs. site-specific litter) did not consistently affect decomposition rates (F₁,₄₀₆=2.16, p=0.14), but modified both the effects of macroinvertebrates (litter type x macroinvertebrates F₁,₄₀₆=20.9, p<0.0001), and habitat type (litter type x habitat type F₃,₄₀₆=161, p<0.0001) on leaf litter decomposition. Finally, the three way interaction between the macroinvertebrate presence, leaf litter type and habitat type caused differing rates of leaf litter decomposition (F₃,₄₀₆=4.86, p=0.003; Fig. 2.11).
We then used our four habitat types to investigate particular land use differences. Using a model simplification procedure (see “Methods”) we found significant effects on leaf litter decomposition of ‘forest conversion’ (orange plantations versus pooled forested habitat: L ratio=12.4, p=0.015), ‘forest fragmentation’ (fragmented forests versus continuous forests: L ratio=13.9, p=0.008) and fragment size (large versus small fragments: L ratio=12.4, p=0.015) on leaf litter decomposition. We therefore maintained all four habitat types in further analyses.

The different types of litter bags allow us to investigate the mechanisms that may be driving leaf litter decomposition rates. For example, we expect that if litter quality effects are driving decomposition rates, we would see larger habitat-type differences in the site-specific litter (Fig. 2.6a). If differences in macroinvertebrates between habitat types are most important, we would expect to see habitat type effects in large litter bags that included invertebrates and smaller differences in those that excluded macroinvertebrates (Fig. 2.6b). Finally, if microclimatic differences between habitat types (or indeed any difference apart from leaf quality and macroinvertebrates) are driving decomposition we would expect the differing decomposition rates to also occur in the small mesh bags with control leaf litter (Fig. 2.6c).

**Forest conversion**

Decomposition rates were faster in orange plantations than in any of the other forest types (Fig. 2.11a). However, the difference between forests and orange plantations occurred primarily in litter bags with site-specific litter (Fig. 2.11a), both in litter bags without macroinvertebrates ($t_{430}=-9.79$, $p<0.0001$) and with macroinvertebrates ($t_{430}=-15.34$, $p<0.0001$). The control leaf litter showed little difference in decomposition between forests and orange plantations in the presence of macroinvertebrates ($t_{430}=1.68$, $p=0.0946$) and none in the absence of macroinvertebrates ($t_{430}=0.90$, $p=0.3686$; Fig. 2.11b). These results suggest that differences in
leaf litter quality, rather than macroinvertebrates or microclimate, are responsible for most of the effect of ‘forest conversion’ on decomposition.

**Forest fragmentation**
Decomposition rates were faster in fragmented forests than in continuous forests. The difference between fragments and continuous forests only occurred in litter bags with site-specific litter (Fig. 2.11a), regardless of macroinvertebrate presence (with macroinvertebrates $t_{426}=2.88$, $p=0.0042$; without macroinvertebrates $t_{426}=2.49$, $p=0.0132$). Control leaf litter showed no difference in decomposition rates between forest fragments and continuous forests (with macroinvertebrates $t_{426}=0.39$, $p=0.6976$; without macroinvertebrates $t_{426}=0.62$, $p=0.5357$; Fig. 2.11b). As with ‘forest conversion’, these results suggest that ‘forest fragmentation’ primarily affects decomposition via changes in leaf quality.

We then further examined the effects of ‘forest fragmentation’ by examining the effect of fragment patch size (large vs. small). In control litter, decomposition was marginally faster in large fragments, but only in the presence of macroinvertebrates (with macroinvertebrates $t_{422}=1.7$, $p=0.0890$; without macroinvertebrates: $t_{422}=0.37$, $p=0.7091$; Fig. 2.11b). There was no difference between large and small fragments in the decomposition of site-specific litter, irrespective of macroinvertebrate presence (with macroinvertebrates $t_{422}=-0.80$, $p=0.4221$; without macroinvertebrates $t_{422}=-1.12$, $p=0.2638$; Fig. 2.11a). These results fit none of the proposed hypotheses. Arguably, dividing fragments into two size classes – large and small – ignores the fact that there is a continuum of fragment sizes. Therefore, we also examined fragment size as a continuous variable, in a model that also included macroinvertebrate presence and litter type as fixed factors and fragment identity as a random factor. There was no improvement over the model that considered categories of fragment size, and the results were
qualitatively similar. However, as will be seen in the next section, effects of area are collinear with effects of distance from edge, which may be the more important driver.

**Distance to forest edge and forest fragment patch area**

Finally, we examined whether leaf litter decomposition within forests was affected by distance to the forest:matrix edge. In continuous forest, leaf litter decomposition was not strongly influenced by distance to edge ($F_{1,107}=3.01$, $p=0.086$). Thus, we were largely successful in eliminating edge effects by situating our continuous forest transects more than 200m from an edge. In orange plantations, distance from nearest forest edge did not explain any variance in decomposition ($F_{1,107}=0.13$, $p=0.72$).

In the fragments, the greatest distances to edge were necessarily constrained to the largest fragments ($r=0.73$, $p=0.017$). We therefore included both fragment area and distance to edge as explanatory factors in models of leaf litter decomposition. Models with both fragment area and distance to edge were significantly better in explaining variance in decomposition rates than models with just fragment area ($L=26.3$, $p<0.0001$), but not significantly better than models with just distance to edge ($L=8.74$, $p=0.068$). This suggests that distance to edge is the more important determinant of decomposition rates, despite the strong collinearity with fragment area. If only distance to edge is considered, there are strong interactions with macroinvertebrate presence ($F_{1,183}=6.34$, $p=0.013$) and litter type ($F_{1,183}=15.8$, $p=0.0001$), and with both factors ($F_{1,183} = 4.18$, $p=0.042$). Inspection of parameter estimates reveals that decomposition increases with distance to edge in the control leaf litter with macroinvertebrate access, but not in site-specific leaf litter or leaf litter without macroinvertebrates. This resulted in a tendency for larger patches, with more litter bags further from the edge, to also have greater decomposition of control litter exposed to macroinvertebrates.
Nutrient cycling
Overall, the availability of macro- and micronutrients was affected by habitat type (PERMANOVA: $F_3=12.2873$, $p=0.001$) but not by macroinvertebrates ($F_1 =0.5595$, $p=0.553$) nor their interaction (habitat type x macroinvertebrate: macronutrients $F_3 =0.3417$, $p=0.910$). We then further explored the effect of habitat type on nutrients with univariate analyses. Habitat type primarily influenced the availability of the macronutrients nitrogen, phosphorus, calcium, magnesium, sulphur and potassium and the micronutrients copper and zinc (Table 2.1). As suggested by the multivariate analysis, macroinvertebrates had little effect on most nutrients, but did increase phosphorus while decreasing manganese. None of the nutrients were individually influenced by the interaction between habitat and macroinvertebrate access (Table 2.1).

Using a model simplification procedure, we found that orange plantations, as compared with pooled forested habitat, had greater availability of the macronutrients nitrogen (Fig. 2.12a), phosphorus (Fig. 2.12b), calcium (Fig. 2.12c), sulphur and potassium and the micronutrients copper and zinc, but decreased the availability of magnesium (Table 2.1). Forest fragments, as compared with continuous forests, had greater availability of only calcium (Fig. 2.12c) and copper (Table 2.1). Most nutrients were unaffected by fragment size, save iron which had higher availability in smaller fragments (Table 2.1).

Discussion
In this study, we examined how landscape difference in northwestern Costa Rica affected detrital decomposition and the subsequent availability of mineral nutrients in the soil. We demonstrated that decomposition of site-specific leaf litter was presumably increased both by forest conversion to orange plantations and fragmentation of previously continuous forest, but largely unaffected by fragment size. Nutrient availability tended to follow the same pattern. The effects of forest conversion and fragmentation on decomposition were most likely attributable to litter quality,
because similar effects were not seen when the litter species was standardized across sites. By contrast, although macroinvertebrates appeared to accelerate decomposition of site-specific litter in orange plantations, differences between habitat types were observed even when macroinvertebrates were excluded from litter bags, and so macroinvertebrate activity alone was unable to account for effects of fragmentation and conversion. Interestingly, macroinvertebrates accelerated decomposition of control litter in large, but not small, fragments. By examining changes in decomposition along a transect from fragment edges to fragment centers, we inferred that this was due to spatial differences in macroinvertebrate feeding preferences. We explain in detail below why this may reflect effects of in situ litter quality on macroinvertebrate behaviour. Finally, although microclimate differed between habitat types, such differences were unlikely to account for differences in decomposition; as decomposition in our most standardised treatment, control litter without macroinvertebrates, was constant across habitat types. We now explore these mechanisms in more detail.

**Leaf quality**
Forest conversion and fragmentation primarily affected litter decomposition effects via differences in the quality of in situ litter. Overall, our study supports a meta-analysis examining plant species traits on six continents (Cornwell et al. 2008) which concluded that litter quality (plant species functional traits) is the strongest predictor of decomposition rates worldwide, much more so than microclimate (Vasconcelos and Laurance 2005) and even macroclimate (Coûteaux et al. 1995; Cornwell et al. 2008; Waring 2012). The ultimate reason for changes in litter quality between our sites is a change in tree composition. Obviously, conversion of intact, often mature forest to orange trees is an extreme change in tree composition. Orange growers optimize nutrient content in orange leaves as leaf nutrients are a robust predictor of fruit yields (Obreza and Morgan 2011). The optimal range of nutrients in orange leaves are 2.5-2.7% dry
mass leaf content for nitrogen, 0.12-0.16% for phosphorus and 1.2-1.7% for potassium (Obreza and Morgan 2011). In our study, privately owned orange leaf litter contained 0.11% ± 0.004 phosphorus. By comparison, leaf nutrients from the forest canopy in Cerrado, Brazil have much lower nutrient concentrations: 1.73% of N, 0.089% of P, and 0.79% of K (Hoffmann et al. 2005). Senescent litter from lowland tropical primary forest have comparable but lower nutrient contents than green forest litter concentrations: 1.5% for N, 0.06% for P and 0.27% for K (Kaspari et al. 2008). In our study, litter from continuous forests had about 0.04% ± 0.01 P content. However, it cannot be assumed that agricultural trees have higher leaf nutrient contents than forest trees. For example, cocoa plantations in Ghana have lower nitrogen content, higher polyphenol concentrations, and higher lignin concentrations than trees in the surrounding forest, and thus slower litter decomposition rates (Dawoe et al. 2010). Thus, conversion of forests to agricultural plantations can either enhance or diminish litter decomposition rates, depending on the leaf traits of the agricultural species.

Our decomposition results suggest that a more subtle change in leaf quality occurs after forest fragmentation. Many of our fragments contained known pioneer species of trees, such as *Cecropia* spp. *Byrsonima crassifolia*, *Conostegia xalapensis*, and *Carica papaya*, which are adapted to fast growth and high light conditions. Previous studies confirm that pioneer tree species tend to produce fast-decaying litter (Xuluc-Tolosa et al. 2003), presumably because the leaves of such species are typically low in chemical or structural defenses (Coley 1983). Indeed, fragments tended to have higher phosphorus content than continuous forests in this study. Fragment size did not affect either the phosphorus content or decomposition of site-specific litter in our study, suggesting similar leaf quality at least over the range of fragment sizes examined (1.32 to 41.59 ha). Because we used leaf litter pooled from the center and edge of the fragment,
our study provided a conservative test of fragment size effects, as edge and center litter is weighted equally despite a lower proportion of edge habitat in larger fragments. However, we note that differences in the decomposition of control litter are suggestive of a change in relative palatability of site-specific litter as a function of distance to forest edge (see “Limitations” below).

Fragment size plays a critical role in tree mortality, which can affect remaining forest structure. For example, tree survival in Amazonian fragments increases with fragment size, from a half-life of 9.3 years in fragments of less than 1 ha, to 28-30 years in fragments of 10-100 ha, to 54 years in interior forests (Laurance et al. 1998). Such shifts in longevity impact plant succession and invasion resistance. In the Amazonian fragments just described, early successional trees were most abundant in small rather than large fragments, and uncommon in intact forests (Laurance et al. 2006). The underlying mechanism here was apparently an edge effect (early successional trees were 3 times more abundant within 100 m of the forest edge) coupled with the fact that smaller fragments have proportionally more edge (Laurance et al. 2006). High tree mortality in small fragments can also allow for the invasion of exotic plants species, as shown, for example, in fragments under 1 ha in Australian dry-open forests (Ross et al. 2002). Together, the shift to early successional and invasive species following forest fragmentation can have substantial impacts on leaf – and hence litter – traits (e.g. Ross et al. 2002).

**Macroinvertebrates**
Macroinvertebrates were responsible for much more of the decomposition of site-specific litter in orange plantations (13.4%) than in continuous (0.6%) and fragmented forests (small 0.95%, large 0.6%), and thus contributed partially to higher litter decomposition in orange plantations (Fig. 2.13). The greater role of macroinvertebrates in the decomposition of orange leaves, as opposed to forest tree leaves, could reflect either habitat differences in the macroinvertebrate community...
or the greater nutritional value of orange leaves. Previous pitfall trapping in the study area has shown differences in the ground insect community between orange plantations and forests, with orange plantations containing fewer insect families with greater skew in abundances between families (Cuke 2012). However, if macroinvertebrate composition alone determined differences between orange plantations and forests, we would expect a similar pattern in the control litter - but such a pattern was not found. Instead, macroinvertebrates may have greater impacts on orange leaves than forest leaves because the former are more palatable. Note that the effects of forest conversion on site-specific litter decomposition cannot be entirely explained by higher macroinvertebrate activity in orange plantations, as orange plantations still had higher decomposition in litter bags that excluded macroinvertebrates.

Macronvertebrates did not appear to contribute to effects of forest fragmentation on the decomposition of site-specific litter. There was very little difference in decomposition between fragmented and continuous forests in either site-specific or control litter. This contrasts with an earlier study at the same site, in which macroinvertebrates were responsible for a significant 8.9% decrease in decomposition following fragmentation, using the same control litter (Cuke 2012). However, Cuke (2012) found this latter result only in the dry season, not the wet season, so it is not surprising that we failed to find this effect in our study, occurring between the two seasons. Indeed, pitfall trapping in the study area reveals only subtle changes in the family composition of ground macroinvertebrates between continuous and fragmented forest (Cuke 2012). Other studies of fragmentation have found that fragmentation results in species replacements in the ground macroinvertebrate community (Driscoll and Weir 2005), potentially conserving functional diversity (e.g. Anderson and Swift 1983; Ruesink and Srivastava 2001).
Macroinvertebrates, although only partial determinants of between-habitat differences in decomposition, were important contributors to total decomposition rates. Overall, excluding macroinvertebrates reduced decomposition rates by 45.8% in our study. This is comparable to a halving of decomposition rates following mesofaunal exclusion in 14 tropical countries (Powers et al. 2009). Our study therefore contributes to the growing recognition of the importance of the macroinvertebrate detritivore community on decomposition rates (Cuke 2012; Powers et al. 2009; Vasconcelos and Laurance 2005).

**Microclimate**
Although both fragmentation and conversion affected the ground microclimate, these differences in microclimate did not translate into differences in the decomposition rates for our most standardised treatment: control leaves without macroinvertebrate effects. Other researchers have also reported differences in forest microclimate that did not translate into difference in litter decomposition, including differences due to fragmentation (Didham 1998; Vasconcelos and Laurance 2005), distance from forest edge (Didham 1998), and successional stage (Vasconcelos and Laurance 2005). Vasconcelos and Laurance (2005) suggest that only extreme levels of disturbance, such as complete clearance, may cause drastic enough microclimate to inhibit the decomposition process in the tropics.

However, differences in litter decomposition associated with forest conversion have been attributed to differences in microclimate. Kurzatkowski et al. (2004) found that decomposition of a common litter, in the absence of macroinvertebrates, was slower in plantations than primary forest, and inferred that microclimate differences were the most parsimonious explanation. In a previous study in this area, microclimate effects were inferred to result in greater litter decomposition in orange plantations than continuous forest (Cuke 2012). Again, this effect
occurred in the wet, rather than late dry season, so it is perhaps not surprising that we did not detect it in our study which occurred between seasons.

Fragmentation effects on microclimate are well documented (Laurence et al. 2002; Murcia 1995). At the edge of new fragments, an increase in light penetration results in greater temperature fluctuations and a decrease in humidity that can penetrate 60m into fragmented forests (Kapos 1989; Murcia 1995; Didham and Lawton 1999). Such microclimate edge effects can cause physiological stress for some trees (particularly shade tolerant species that are now part of the edge), resulting in leaf senescence and tree death (Lovejoy et al. 1986; Ferreira and Laurance 1997). Opening up a forest edge allows winds to penetrate further into the remnant forest (greater than 300m), blowing down the remaining large trees (Laurance 1997). These tree falls create further disturbances and forest gaps which result in change in light intensity, humidity, temperature and moisture on the forest floor (Laurance et al. 1998). These microclimate changes can affect forest structure and the decomposer community. We noted greater light penetration, higher temperatures and more dead trees in small fragments than continuous forests in our study, but apparently these microclimate changes were not enough to influence litter decomposition. It is possible that the orange plantations partially buffer fragmentation effects on microclimate (Laurance et al. 2002). For example, Didham and Lawton (1999) found that fragments that were surrounded by 5-10m tall trees had less extreme changes in microclimate. Finally the age of the fragment also can affect the re-closure of forest edges (Laurance et al. 2002). Our fragments were greater than 20 years old which may have allowed them to buffer the microclimate effects on decomposition rates by having more sealed edges.

Forest conversion to agriculture results in more extreme versions of the microclimate changes seen with fragmentation: greater runoff and soil erosion from rain impact (Bisong et al.
2012), higher soil temperatures (Martius et al. 2004), greater fluctuations in temperature and humidity (Bisong et al. 2012; Martius et al. 2004), and lower relative humidity (Bisong et al. 2012). However, agricultural crops also have substantial effects on microclimate. In agricultural plantations, temperature is dependent on canopy structure (Martius et al. 2004). For example, when shade trees are added to coffee plantations, wind speeds are reduced by 35% and maximum air temperature drops (Pezzopane et al. 2011). In this study, the soil was generally much drier and compact under orange plantations, and the air temperatures were higher and more variable. However, these changes were not drastic enough in the early wet season to slow decomposition rates in our plantations sites relative to the enhancement due to litter quality and macroinvertebrate effects.

**Fragment area and distance to forest edge effects**

In forest fragments both area and distance to edge can be important factors that affect decomposition. Forest fragments can contain two types of habitat; edge habitat and interior (core) habitat. As forest fragment area increases, the area of interior compared to edge habitat increases (Saunders et al. 2001). Interior and edge habitats contain different species, and as area increases, the proportion of shade tolerant, rare and old growth species increases as the proportion of light loving, pioneer species decreases (Laurance 1991; Hill and Curran 2003). Therefore larger forest fragments would contain microhabitat characteristics more similar to that of continuous forest than smaller fragments, which contain more edge habitat. Tree species can also vary widely in litter quality (Cornwell et al. 2008). Changes in tree species diversity will therefore alter forest floor litter mixtures which will have consequences for the rates and patterns of litter decomposition and litter utilization by detritivores and microbes (Gessner et al. 2010). Based on previous literature, at least one of our small (1.32 ha) fragments may not have contained any interior habitat resembling continuous forests.
Distance-to-edge effects were mainly observed in control leaf litter with macroinvertebrate access permitted. Here the control leaf litter decomposed faster when located further into the fragment interior compared to the edge. However, this same pattern was not observed in either the control litter that excluded macroinvertebrates or the site-specific litter that allowed macroinvertebrate access. We suspect that this effect is due to macroinvertebrate preference coupled with a shifting baseline in litter quality: the further from the edge, the more the macroinvertebrates utilize the more palatable leaves (control litter) compared to site-specific litter, as a result of leaf quality changes towards the interior of larger fragments. Thus, although we attempted to remove leaf quality differences between sites by examining decomposition of a standard species of litter, detritivore consumption of this standard litter may be influenced by the relative quality of the surrounding litter. Food choice experiments demonstrate that detritivores have highly selective feeding behaviours (Suberkropp 1992; Graça 2001). Macroinvertebrates are more likely to select high quality, palatable leaves when given a mix of lower and higher quality litter within the same site (Swan and Palmer 2006). For example, in a study of leaf-cutting ants in early secondary forest and old growth tropical forests, leaf-cutting ants selected leaves from pioneer species eight times more often than leaves from shade tolerant leaf species (Farji-Brener 2001). Thus our control litter may not always be a control in the absolute sense as its perceived palatability is a function of the quality of the surrounding \textit{in situ} litter. As consumption of control litter by macroinvertebrates increased with distance from fragment edge, and because large fragments had more area distant from edges, control litter tended (0.10>p>0.05) to be consumed by macroinvertebrates at a higher rate in large fragments than in small fragments.
Limitations
We have just described how differences between the control litter quality and background litter quality can complicate interpretations of macroinvertebrate consumption rates. The disadvantage of a non-absolute control means that there is inevitably some error in our attempts to “remove” the effects of leaf quality on between-habitat differences in decomposition. However, this uncertainty should be restricted to the litter bags that permitted macroinvertebrate access, and so should not influence our conclusion that microclimate was generally unimportant in explaining habitat differences.

There are additional well-documented limitations to the litter bag method. Mesh size not only determines macroinvertebrate access, but also the likelihood of fine particle loss, which can confound attempts to isolate effects of macroinvertebrates. Litter bags may also alter the microhabitat conditions within the litter, altering the decomposition process (e.g., light intensity, moisture, waterflow regimes, litter density and chemical conditions) (Schnitzer and Neely 2000). Decomposition is measured from change in the litter that remains within the bag, and ignores non-biological loss such as the low molecular weight organic compounds that leach out, or the other particles that fall through, and therefore is inevitably overestimated (Reddy et al. 1999). However, despite the limitations of litter bags they are widely accepted for investigating terrestrial decomposition processes.

The space-for-time substitution in our study design implicitly assumes that orange plantations and forest fragment sites were, prior to human disturbance, identical in all respects to the original continuous forests. However, this may not be the case if forest fragments were not randomly located. For example, forest fragments may have been intentionally not converted to orange plantations if they did not provide ideal agricultural conditions (e.g. uneven slopes or contain swamps unacceptable for agricultural crops and machinery). Similarly, the locations
containing orange plantations may not be random, for example, these may have been chosen over current forested habitat as these sites were naturally more productive. Finally, the continuous forest sites included several within the boundaries of the protected Guanacaste National Park, and historical reasons for the designation of this park boundary may influence site characteristics. Although we can never fully prove that our sample sites are random representations of the landscape, we did ensure that the sites were randomly located with respect to the dominant climate and spatial gradients in our landscape, as represented by elevation, latitude, longitude.

A second limitation of space-for-time substitutions is the inability to account for extinction debts. Species may be unable to replace themselves in a fragment, but still be present and contributing to the ecosystem. For example, long lived trees may be present and producing leaf litter, however environmental conditions post-fragmentation may be unacceptable for seedling survival to replace parent trees. Only long-term studies can witness the changing ecosystem dynamics of fragments as this extinction debt is slowly diminished over time.

**Nutrients**

Orange plantations generally had higher nutrient availability when compared to forests, but there was large variation within the orange plantations. We selected orange plantations from a representative of the orange plantations located in the study area; four orange plantations were located within the Del Oro properties and two orange plantations were privately owned and operated. Decomposition rates did not appear to be as variable as the nutrient availability. There are two likely possibilities for this high variability of nutrient availability; first, understory differences additionally impact nutrient availability (e.g. differences in soil moisture) or second, management practices additionally influence the availability of nutrients input into the systems. Regarding the second possibility, the Del Oro plantations generally had higher nutrient
availability than the privately owned plantations, for example phosphorus. Phosphorus is generally low in tropical forests, however, 4 of the 6 orange plantations (all Del Oro plantations) had elevated phosphorus availability in comparison to the forests. This could be due to fertilization regimes implemented to increase fruit production. However, we currently have no information to confirm or refute that this may be a possible explanation based on our knowledge of the agricultural practices at these plantations.

The elevated phosphorous levels in this landscape could aid detritivore abundance and therefore decomposition rates. In a study in old growth tropical forests, detritivore abundance was linked to soil and litter phosphorus levels (McGlynn et al. 2007). Forest fragmentation also resulted in increased availability of select nutrients, particularly calcium, copper and (marginally) sulphur. Several studies have shown that calcium in litter increases closer to the edge of forests (Vasconcelos and Luizão 2004). This may be linked to changes in tree growth strategy, whereby roots of pioneer species mobilize higher amounts of calcium from the soil (Lucas et al. 1993 as cited in Vasconcelos and Luizão 2004). Sulphur has been found in previous studies to increase at forest edges because of the edges ability to trap anthropogenic pollution (Weathers et al. 2001), potentially from fertilizers or herbicides used for management practises in nearby agricultural areas (Murcia 1995).

**Decomposition rates at odds with carbon storage**

Any changes in decomposition rates can have widespread effects on these tropical ecosystems in terms of productivity and ecosystem functioning. Both forest fragments and orange plantations had elevated nutrient availability and higher decomposition rates, and one interpretation of these results is that fragmentation and conversion therefore increases soil fertility. However, nutrient mineralization is only one aspect of the decomposition process. Decomposition also affects soil fertility through the process of humification, caused by the accumulation of organic carbon (slow
to breakdown organic matter) in the soil. Increased rates of decomposition are said to be at direct odds with the humification process and storage of organic carbon within soils. Humus is important because it can greatly increase cation exchange capacity and it positively impacts the nutrient availability in the soil over time (Berg and McClaugherty 2008). For example, humus can be a source of carbon for soil microorganisms which contribute to soil weathering and nutrient availability (Berg and McClaugherty 2008). In the orange fields especially, losing the humus layer in the soil will lead to increased nutrient leaching and the soil can lose its ability to retain moisture and nutrients in the long term. Decomposition of soil carbon and humus is generally slow due to the low quality of the detrital resource for detritivores (Prescott 2005a).

High decomposition rates in this study, especially in orange plantations, resulted in all but a few leaf veins left in the litter bags after only 3-8 weeks. Thus, hardly any litter was left in these bags to undergo the humification process. Some of these orange plantations already had cracking, dry and hard top layers of soil (Fig. 2.14). Therefore increased rates of decomposition and the lack of humus could be, in fact, decreasing site fertility if the mobilized nutrients are being leached from the soil rather than fueling primary productivity.

Humification is not only important in affecting soil fertility and structure, but also in terms of the ecosystem carbon budget. Tropical forests account for approximately 59% of the global carbon pools found in forested ecosystems, highlighting their importance in the world carbon budget (Dixon et al. 1994). Tropical ecosystems store approximately 340 billion tons of carbon (Gibbs et al. 2007). However, tropical deforestation releases approximately 2.9 billion tons of carbon a year from these ecosystems (Pan et al. 2011). Currently, we do not know if tropical forests are net carbon sources or carbon sinks (Clark et al. 2001; Clark 2004). Data is extremely limited regarding net primary production in tropical forests (Clark et al. 2001), which
is the main driver of carbon sequestration. The decomposition process transforms nearly as much carbon as the process of photosynthesis but decomposition occurs on or below ground (Berg and McClaugherty 2008). Put simply, carbon pools are a balance of carbon input into the system from primary production, and the output from the system by the decomposition process and other processes such as leaching (Amundson 2001). Plant functional traits can strongly drive carbon storage by regulating carbon assimilation, stored belowground as biomass, and release through soil respiration (De Deyn 2008). Plant functional traits can be categorized based on plant history traits such as fast growing or slow growing species. These plant functional traits lead to differences in the physical and chemical composition of litter inputs into the decomposition process. Fast growing, short-lived species allocate the majority of carbon to photosynthetic structures of higher nutrient content, which generally decompose more quickly (Aerts and Chapin 2000). But, slow growing, long-lived species allocate the majority of carbon to structure and plant defenses and therefore produce recalcitrant, nutrient poor, litter (Aerts and Chapin 2000) and more aboveground carbon stored as biomass. Recalcitrant litter withholds carbon in the form of lignin by reducing microbial activity, enhancing carbon sequestration due to accumulation in the soil layers overtime as humus (de Boer et al. 2005; De Deyn et al. 2008).

While fast growing species are metabolically more active, contributing to higher rates of respiration which results in carbon loss, their litter is generally more palatable for detritivores and easily decomposable overall, furthering carbon loss (De Deyn et al. 2008). Therefore, a shift from slow growing species in the continuous forests to faster growing pioneer species, and agricultural groups selected for high yielding production can see a shift in the landscapes carbon storage abilities due to shifts in plant traits and their effects on biomass and decomposition rates. It is important to keep in mind that leaf litter and macroinvertebrates only represent the
aboveground biota that can affect the carbon cycle: root decomposition and microorganisms belowground also play a major role in carbon storage. The amount of humus that is in the soil depends on the microbial fauna’s inability to break down the recalcitrant litter.

Therefore, the effects of decomposition on ecosystem functioning depend on which functions are considered (soil fertility vs. carbon storage), and the interplay between humification, microbial biomass and nutrient availability. For example, it could be beneficial - hypothetically- to have a marginally increased rate of decomposition due to some shifts in plant traits that allows for a small increase in soil nutrient availability while still containing recalcitrant litter (soil carbon) that is slow decomposing allowing soils to be more fertile by holding more nutrients in humus and releasing them slowly overtime. Considering all the individual processes occurring simultaneously in the process of decomposition, it is nearly impossible to simplify whether increased litter decompositions rates are “good” or “bad” for ecosystem function, as litter decomposition is multifaceted and interconnected with many other ecosystem processes occurring simultaneously in complex ways.

**Implications**
In this study we documented effects of forest conversion to orange plantations, forest fragmentation and fragment size on litter decomposition, primarily through changes in litter quality. We presume that in the case of forest fragmentation, changes in microclimate are responsible for changes in tree composition. In the case of forest conversion, macroinvertebrates were important in translating leaf quality differences into changed decomposition rates. As tropical forests are becoming more fragmented and isolated it is important to understand how the resultant shift in litter quality may affect remnant forest productivity and biota. This study shows that landscape change may initiate an aboveground-belowground feedback whereby altered aboveground plant communities have consequences for the belowground processes of litter
decomposition and nutrient mineralization which subsequently fuels the aboveground community. The shift in litter quality in our study area has increased the rate of decomposition in remnant forest patches and orange plantations. Such changes in decomposition rates and forest structure will affect carbon dioxide emissions and carbon storage (Chapin et al. 2002). Previous studies have shown that increasing rates of decomposition will increase carbon dioxide emissions into the atmosphere which will continue to fuel climate change (Chapin et al. 2002). Our study shows increases in the rate of decomposition and nutrient availability due to landscape differences (a positive ecosystem service), but it is critical to consider that in some contexts nutrient cycling is directly at odds with nutrient storage (e.g., carbon storage, another ecosystem service).
## Tables and Figures

Table 2.1. ANOVA results for nutrient availability under site-specific litter bags. Where conversion effects are examined by comparing pooled forests (F) to orange plantations (O), fragmentation effects are examined by comparing pooled forest fragments (P) to continuous forests (I), and fragment size compares large fragments (L) to small fragments (S).

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45
Figure 2.1. Map of the study area with the 22 sites outlined (I is continuous forest (green), O is orange plantation (orange), L is large fragment and S is small fragment (pink)). Dots represent the centers (end of transect) in each site.
Figure 2.2. An example of a small (a) and large (b) fragmented forest patch in the study area.

Figure 2.3. An example of one of the continuous forest sites.
Figure 2.4. An example of an orange plantation in Del Oro (a) and an example of a privately owned orange plantation (b).
Figure 2.5. Three mechanisms that can affect leaf litter decomposition and nutrient cycling.

Figure 2.6. Predicted outcomes if differences in decomposition in hypothetical Habitat A and Habitat B were due to (a) habitat-specific differences in leaf quality, (b) habitat-specific differences in macroinvertebrates, (c) microclimate or other habitat differences independent of leaf quality and macroinvertebrates. +MI represents treatments with macroinvertebrate access, -MI represents treatments that exclude macroinvertebrates, triangles represent site-specific litter treatments, circles represent control litter treatments.
Figure 2.7. Placement of transect and decomposition plots in an example fragment (site L4).

Figure 2.8. The 9 mm leaf litter bags containing forest litter (small fragment), control litter (pasture litter), and orange plantation litter.
Figure 2.9. Phosphorous content of leaf litter fall, measured as percentage, from continuous forests, large fragments, small fragments, pasture trees (control litter), and orange plantations.

Figure 2.10. (a) Habitat effects on microclimate variables including maximum daily, minimum daily and daily average temperature (°C) and relative humidity (%) in the study area from August 4th to September 2nd 2011. (b) Temperature (°C) (measured every 30 minutes) throughout the last half of the study period (Aug 4th – Sept 2nd) for a typical orange plantation (site O3), small fragment (site PSP), large fragment (site L4) and continuous forest (site I5).
Figure 2.11. Decomposition, measured as exponential decay coefficients of litter mass over time, for four habitat types, in litter bags with (a) site-specific litter and (b) control litter. Grey bars represent macroinvertebrate presence and white bars represent absence of macroinvertebrates.
Figure 2.12. Habitat types and the availability of soil nutrients: (a) total nitrogen, (b) phosphorus, (c) calcium (white bars +MI, grey bars – MI).
Figure 2.13. Macroinvertebrate effect on decomposition decay coefficients, expressed as a percentage, for the four habitats and two litter types. Black bars represent effects on site-specific litter and grey bars represent effects on control litter. Error bars are 95% CI, so overlapping CIs are not different from each other.

Figure 2.14. An example of the dry, bare topsoil in a privately owned orange plantation.
Chapter 3. General conclusion
In northwestern Costa Rica, the landscape has seen rapid change due to forest fragmentation and land conversion to orange plantations. In this study we examined the effects of forest fragmentation and forest conversion to orange plantations on leaf litter decomposition and nutrient cycling. Both conversion to orange plantations and forest fragmentation increased leaf litter decomposition rates, but fragment size had little discernible effect. This was generally also the trend for the measured nutrients. Our study highlights the importance of litter quality effects on decomposition rates at the landscape and site scale, as it was the change in litter quality that caused the increase in decomposition rates. There was no difference in decomposition rates of control litter between habitat types which indicates that although there were microclimate differences between habitats, microclimate was likely not a direct determinant of decomposition rates. Finally, macroinvertebrate access increased decomposition rates, however, this increase was similar across all sites. When examining site-specific litter, macroinvertebrates increased the rate of decomposition of orange litter compared to the other forest types but this pattern was seen in the absence of macroinvertebrates too. Therefore, macroinvertebrates are important contributors to the decomposition process but do not fully explain the differences in decomposition rates between forest types observed in this study. The distance to forest edge in the forest fragments impacted macroinvertebrate feeding behaviour, thus indirectly impacting decomposition rates. The deeper into the forest fragments, the more the macroinvertebrates appeared to take advantage of the more palatable control litter compared to site-specific litter. This edge effect was not seen in our continuous forests.
Importance of fragments and plantations
The concept of “countryside biogeography”, pioneered by Gretchen Daily and colleagues, emphasizes the importance of forest fragments in preserving biodiversity (Daily et al. 2001; Ricketts et al. 2001; Daily et al. 2003; Mayfield and Daily 2005). Large fragments generally contain greater species and habitat diversity compared to smaller fragments. However, several small fragments could contain greater habitat diversity than one large fragment due to greater area coverage (Saunders et al. 1991). Species that require several types of habitats generally require large areas of land to survive while species that have less complex habitat requirements and localized populations can generally survive in smaller areas (Saunders et al. 1991). Other studies have shown the importance of small fragments of at least >1 ha in tropical lowland Costa Rican forests which have proven to be important for overwintering migratory wood thrushes (Roberts 2011). Wood thrushes that arrive late may not be able to find territories in nearby protected continuous forest and therefore are forced to enter such unprotected forest fragments in the surrounding agricultural matrix to survive and overwinter (Roberts 2011). Our orange plantations were frequented by numerous animals from remnant forests. Frogs and tadpoles inhabited puddles created by machinery in the orange plantations, seed dispersers such as agoutis were frequently seen taking advantage of fallen oranges and fleeing back to the safety of remnant fragments when discovered, and many rabbits and even coatis were also sighted. Numerous bird and butterfly species were seen frequently in the orange plantations, including parrots, toucans, oropendulas, squirrel cuckoos, magpie jays, king vultures and a barn owl that was seen on occasion on fence posts at a newly planted orange plantation and flying over a small forest fragment and further on towards the continuous forest. Even bullet ants and leaf cutter ants lead trails from orange plantations back to their nests in remnant forest patches. Unfortunately, any landscape frequented by humans can have detrimental effects on local fauna as well. For
example, during fieldwork we found that a 5-foot long boa had been slashed with a machete in one plantation, and in another, a local farm owner wanted to kill a snake on an orange tree, even though it was a harmless slug-eater species. Enhancing the knowledge of local farmers may aid in biodiversity conservation and lessen disturbance in these changed landscapes. Unfortunately, remnant forest fragments surrounding orange plantations had evidence of illegal poaching and numerous Great Curassow (turkey-like bird) had been shot during our study. A local land manager at one of the continuous forests told us he had seen a tapir and her calf, but he was concerned that they may get shot if found frequenting outside of the safety of the forest. The landowner of a large fragment in our study area cautioned us of illegal hunting for deer in that fragment. Our landscape followed the usual trends expected from continuous forests, forest fragments and orange plantations in terms of animal composition. Evidence of larger mammals was only found in continuous forests, including a jaguarundi sighting, and other feline, tapir and peccary tracks. Manakins (white collared and red capped) were typically spotted lekking only in continuous forests, with the exception of a single sighting in a small fragment. We still saw mixed flocks of birds foraging (a behaviour more typical of continuous landscapes) in one of our large fragments. Common tent bats were often seen roosting in one of our large fragments. Monkeys were spotted more consistently in continuous forests but also a number of our fragments were frequented by howler monkey and spider monkeys. Coatis were spotted in forest fragments, leaving orange plantations and in continuous forest. These observations highlight the importance for both forest fragments and orange plantations for local biodiversity persistence. Thus, small privately owned fragments in Costa Rica comprise important habitats and do not necessarily act as species ‘sinks’ within the landscape. However, impacts on species prevalence in forest fragmentation can depend on the species’ mobility.
The species important for leaf litter decomposition are invertebrate detritivores; they are small, often perceive forest edges as barriers, and have localized populations. We did not find effects on decomposition rates due to microclimate change and it did not appear that macroinvertebrates were hindered in their functional ability to aid in decomposition rates between forest fragments, orange plantations and continuous forests, in contrast to previous studies which found decreases in macroinvertebrate fauna (Cuke 2012). If macroinvertebrate compositional changes were driving the changes in leaf litter decomposition, we would have expected to see similar patterns in both site-specific leaf litter and control litter, but we did not. Also, because our fragments are relatively small in comparison to other studies (<41.6 ha in size) if there were compositional changes effects on litter decomposition we would have expected to find them at this scale of remnant fragments. Therefore, it seems that macroinvertebrates’ role in leaf litter decomposition primarily depends on leaf palatability.

**Importance of carbon storage in changing landscapes**

We have highlighted the importance of litter quality on leaf litter decomposition, the main effect between forest types in our study area, in this thesis. However, litter quality and other plant traits are extremely important in terms of nutrient and carbon cycling. Decaying above- and belowground plant matter results in organic soil carbon (De Deyn et al. 2008). 45% of the total global carbon stock contained in terrestrial vegetation is contained in tropical forests (Bolin and Sukumar 2000) and therefore these forests play a major role in global carbon cycling. Any change to these forests in compositional structure (not to mention deforestation) may contribute to anthropogenic greenhouse gas emissions (IPCC 2000). The differences in leaf litter quality between our 3 forest habitats (no differences between sizes of fragments) highlight the changes in plant functional traits due to disturbances caused by forest fragmentation and forest
conversion to orange plantation. It is these plant functional traits that control carbon storage and therefore will impact the global carbon cycle (De Deyn et al. 2008). Previous studies have shown that increasing rates of decomposition will increase carbon dioxide emissions into the atmosphere which will continue to fuel climate change (Chapin et al. 2002). In this study this shift in decomposition rate in site-specific litter is a consequence of the change in tree community dynamics caused by the effects of forest fragmentation as described earlier and of the different leaf traits in the orange litter compared to that of continuous litter. In forest fragments the edge habitat generally selects for different plant response traits than that in the interior/core habitat. Forest fragments generally show a shift from slower growing, shade tolerant, long-lived tree species to that of greater light loving, fast growing, short-lived pioneer species. The advantage in terms of carbon storage of this shift to fast growing species is that they generally have higher photosynthetic rates than slow growing plants, but the disadvantage is that these shorter life span results in lower carbon concentrations and less biomass in above and belowground plant matter (Aerts and Chapin 2000). Unsurprisingly, this shift in plant functional response traits could result in a change in carbon storage in these remnant forest fragments and citrus plantations. The slow growing, long-lived species from interior forests tend to have recalcitrant litter that is nutrient poor (Aerts and Chapin 2000), which is beneficial for carbon sequestration due to the increased length of time required to break down lignin, polyphenols and tannins within the soil (Hättenschwiler and Vitousek 2000). Also, long lived trees species tend to hold more carbon as biomass above ground than short-lived species. In contrast, the shift of traits to fast growing, short-lived pioneer species in forest fragments due to microclimate changes could result in allocating their carbon to higher photosynthetic structure of low density but with higher nutrient contents (Aerts and Chapin 2000). As seen in our study these higher nutrient
content leaves increase decomposition rates overall. In addition, this guild of tree species is more active metabolically and thus loses greater amounts of carbon during respiration than their slow growing counterparts (De Deyn et al. 2008). Increased detrital decomposition has the potential to also increase soil carbon loss, though this is yet to be tested (De Deyn et al. 2008). It has been concluded in a review by De Deyn et al. (2008) that to prevent carbon loss at the community level there will have to be a combination of plant traits that resist disturbance until quick re-colonization traits permit recovery of resources. Therefore, I highlight the importance of forest fragments and orange plantations in the carbon cycle. Though our small fragments, which have few long-lived interior species, may act more like carbon sources (depending on the level of disturbance), larger fragments may be very useful in preventing carbon losses. Large fragments may be able to balance the effects of edge species which have a greater photosynthetic ability with the effects of those species better for carbon storage that are found in the interior. Of course, I would speculate that any type of forest is better than no forest at all in terms of carbon storage and in general for biodiversity and connectivity. Small forest fragments, for example, can act as seed rain for tree species to nearby neighbouring forest fragments. Unfortunately, despite numerous studies on tropical forest ecosystems there are currently insufficient data to even establish if the world’s tropical rainforests are net carbon sinks or net carbon sources (Clark 2004). The estimates of aboveground biomass in these forests are extremely inaccurate at large spatial scales (Houghton 2005). Fragmentation effects on carbon emissions could be important for individual landscapes (Laurance et al. 1998). It has been estimated that 1-7% of current estimates of global carbon emissions in tropical landscapes are too low based on biomass alterations in fragmented forests not being considered in these estimates (Laurance et al. 1998). It has been suggested that global warming alone will cause tropical old-growth forests to be
sources of increased atmospheric carbon dioxide (Clark 2004). Therefore, temperature increases in these fragmented forests may already be raising carbon dioxide emissions in addition to shifts in litter traits. In summary, although others have written about nutrient cycling as a positive ecosystem service, it is critical to note that in some senses nutrient cycling is directly at odds with carbon storage and sequestration – another important ecosystem service. In other words, increases in the availability of nutrients due to increases in litter decomposition may be a positive impact in terms of nutrient cycling, however, the increased rate of breakdown of standing litter is a negative impact in terms of carbon storage and aids in carbon emissions.

**Orange plantations: Potential benefits of tree crops**

Orange plantations may be acting as above ground carbon sinks. In a temperate apple orchard most carbon sequestered went to fruit production (49% NPP) and then organic materials that entered the decomposition cycle accounted for 46% and only finally only 5% NPP was in standing biomass (Zanotelli et al. 2012). Overall the apple orchard had a greater gross primary production that was comparable to the natural forests. The carbon use efficiency of the orchard overall, at the local scale, was greater than nearby forests, most likely due to more carbon being allocated to apples that were then harvested and removed from the ecosystem, making the orchard a carbon sink (Zanotelli et al. 2012). A temperate forest or apple orchard has a distinct growing season, whereas our orange plantations are in the tropics. However, carbon may be leaving the orange plantation ecosystem via fruit harvesting during different times of the year. Orange trees are much smaller than forest trees and are selected for orange production and then the oranges are removed from the ecosystem during harvesting. Also, generally any type of agriculture comes with management practises such as the use of machinery for tillage, spraying, and irrigation and this management will also influence carbon sequestration and emission,
nutrient cycling, and biodiversity. In West Ghana, in a 25-year old orange plantation the carbon content was estimated to be 76.3 tC/ha/yr, an accumulation rate of 3.1 tC/ha/yr (Kongsager et al. 2012). However, converting old growth forests to plantations has typically resulted in large carbon losses, except in 40 yr old rubber tree plantations (Konsager et al. 2012). A more beneficial approach to agricultural development in tropical ecosystems is to convert already degraded or non-tree crops to tree crop plantations, this generally results in preventing carbon from leaving the ecosystem and creates corridors between forest remnants.

**Future directions**

Future studies in this system of forest fragments and orange plantations should include quantitative measurements of the standing biomass over time. Previous studies have found that less biomass is present along fragment edges than in fragment interiors, which appeared to be the case in our study fragments (personal observation). However, forest fragments are very dynamic and have different successional stages over time. Measuring the standing biomass in these remnant fragments could aid in the understanding of shifts in biomass due to fragmentation and how these shifts relate to the global carbon budget. Estimating aboveground biomass and net primary productivity in the orange plantations would further our understanding of the agricultural component of landscape carbon storage. Also, more work on the remnant fragments and tree plantations in Costa Rica could aid in REDD (reducing emissions from deforestation and forest degradation) incentives (or other such incentives) for the local private landowners and corporations to protect these remnant forests and manage plantations effectively, as most fragments and some of the orange plantations were privately owned and this could aid from community/landowners involvement in the protection and management of these ecosystems.
This study highlighted the importance of litter quality, however, there is more that needs to be disentangled in this landscape. The current study examined litter decomposition of site-specific and control litter on an edge to center (interior) transect to account for potential edge effects in our forest fragments. We found that macroinvertebrates appeared to show behavioural changes in feeding behaviour on control litter. However, because our site-specific litter was only a representation of each site (with a mix of litter sample from one location in the center and edge of the site in each bag) it does not mirror litter changes that would be expected to occur based on previous literature from forest edge to interior. Therefore, the next step in examining the impacts of edge effects on the decomposition of site-specific litter would be to examine litter decomposition of site-specific litter as a function of the edge-to-center transition. Each plot should contain litter from that plot. I feel our results on site-specific litter in terms of edge effects to be conservative in this regard due to each forest fragment containing the same site-specific mixture per site and not according to potential litter changes from the edge to center of the fragments.

**Conclusion**
I suggest we should consider thinking of forest fragments and agricultural landscapes as more than just ‘doomed’ and instead consider the conservation potential of these areas. Previous research on ecological and biodiversity studies have focused on protected areas and reserves with minimal impact from human populations (Fazey et al. 2005). However, a more realistic approach to present-day dilemmas in tropical ecosystems is to also shift more focus on biodiversity and ecosystem processes in landscapes that are modified and managed by human populations for commercial and traditional purposes (Chazdon et al. 2009). This research has furthered our understanding of the vital ecosystem function of leaf litter decomposition and
nutrient cycling in protected continuous forest, unprotected forest fragment remnants, and commercially managed and privately operated orange plantations in tropical lowland Costa Rica.
References


Ross, K.A., B.J. Fox and M.D. Fox. 2002. Changes to plant species richness in forest fragments: fragment age, disturbance and fire history may be as important as area. Journal of Biogeography 29: 749-765.


Appendix

Table A.1. ANOVA results for microclimate data in the study sites

<table>
<thead>
<tr>
<th>Model Type</th>
<th>Daily Temperature</th>
<th>Daily Humidity</th>
</tr>
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<tbody>
<tr>
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<td>Average</td>
<td>Maximum</td>
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<tr>
<td><strong>Full Model ANOVA</strong></td>
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<td></td>
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<tr>
<td>Effect</td>
<td>df</td>
<td>L ratio</td>
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<td></td>
<td></td>
<td>15.9</td>
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<tr>
<td><strong>Model simplification and comparison ANOVA</strong></td>
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<td></td>
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<tr>
<td>Effect</td>
<td>df</td>
<td>L ratio</td>
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<td>Fragment size</td>
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