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RRH: Recovering Decomposition Rates by Invertebrates

Title:

‘Recovery of decomposition rates and decomposer invertebrates during rainforest restoration on disused pasture’

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ABSTRACT

Converting forest to pasture can alter the roles of biota in ecosystem functioning, while vegetation restoration should arguably assist functional recovery. Since tests of this are scarce, this study quantifies both litter decomposition rates and their association with decomposer invertebrates, across 25 sites representing different phases of deforestation and subsequent reforestation of rainforest. Open and closed (to exclude macro-invertebrates) mesh bags containing forest leaves were exposed in the field for up to eight months, and invertebrates were extracted from separate collections of ground surface litter. Sites spanned five vegetation categories (five sites in each): reference states of both old-growth forest and grazed-pasture; unassisted woody regrowth aged 20-50 years on former pasture; and assisted regeneration aged 1-3 and 5-10 years after interventions were applied to similar regrowth. Decomposition rates in open-bags were about 50 % slower in pasture than old-growth forest, and abundances of macro- and meso-decomposer invertebrates were 95 % and 77 % lower respectively. However, in all restoration site-types, decomposition rates had recovered to 83 % of old-growth values, and abundances of invertebrate decomposers were similar in old-growth forest. Decomposer community composition at a broad taxonomic level differed strongly between pasture and all other vegetation types. Exclusion of macro-invertebrates decreased decomposition rates by only about 3.1 %, but decomposition rates in open-bags were significantly correlated (across sites) with abundances of both macro- and meso-decomposers, most strongly so for meso-decomposers. Drawing useful generalisations across studies is impeded by differing methodologies and because few include both agricultural and forest reference sites.

Key words:

detritivore; ecosystem function; succession; regeneration; reforestation; insect; litter; sub-tropical Australia.

FORESTS THROUGHOUT THE TROPICS HAVE BEEN EXTENSIVELY CLEARED FOR PASTURE OVER the last century and continue to experience high levels of loss (Hansen *et al.* 2013). Many pastures are subsequently abandoned, providing the potential for forests to regenerate naturally (Chazdon *et al.* 2009; Wright 2005). However, deforestation degrades critical underlying ecosystem processes affecting nutrient cycling, such as litter decomposition. Lasting effects of pasture establishment, such as soil compaction and interactions with pasture grasses and herbs can reduce the capacity of many native forest trees to regenerate naturally (Erskine *et al.* 2007; Hättenschwiler *et al.* 2005; Zimmerman *et al.* 2007). In such instances a passive restoration approach of simply excluding livestock to allow unassisted recovery may not be sufficient, and active restoration may be needed to assist natural regeneration (Chazdon 2008). Assisted natural regeneration (ANR) approaches aim to accelerate recovery by removing barriers to forest redevelopment such as seedling predation by livestock or competition from invasive plants (Elliott *et al.* 2013; Uebel *et al.* 2017).

Fall of leaves to form litter is a dominant pathway for returning nutrients from trees to soil and can potentially contribute 69-87 % of essential elements required for plant growth (Waring and Schlesinger 1985). However, litter breakdown first must take place to transform the nutrients held in litter into a chemical form available to plants. Decomposition is a complex process and requires a specific set of abiotic and biotic conditions to occur. Important drivers reported to influence litter decomposition rates include: local climate variables such as precipitation and temperature (Wall *et al.* 2008; Zhang *et al.* 2015); changes in micro-climatic conditions (again, primarily moisture and temperature) associated with canopy openness and solar exposure (Paudel *et al.* 2015); plant species traits such as nitrogen, carbon, and lignin content (Cornwell *et al.* 2008; Hättenschwiler *et al.* 2011); and the diversity of resident invertebrates and microbial communities (Gessner *et al.* 2010).

Invertebrate decomposers are of particular importance because they can accelerate the rate of decomposition (Frouz 2018). Macro-invertebrate decomposers (>1 mm length, such as millipedes, isopods, and earthworms) consume and break up substantial amounts of leaf litter into smaller fragments (Wardle *et al.* 2002). Meso-invertebrates (<1 mm length, such as Collembola) also transform litter into considerably smaller fragments, however on a smaller scale (Hättenschwiler *et al.* 2005). The physical breakdown of litter by invertebrates also inoculates microbes onto fresh litter surfaces and renders it into sufficiently small particles for microbes to perform the final stages of decomposition. Litter is converted into nutrients via biochemical reactions by microbes such as denitrifying and nitrogen-fixing bacteria and fungi (Wardle *et al.* 2004). However, these decomposition processes are likely to be disrupted by the loss of vegetation and soil degradation when forest is converted to pasture (Frouz 2018; Lorenzo *et al.* 2014). Abundances of invertebrate decomposers can also decline, and their composition can alter (Grimbacher *et al.* 2006) and rate of decomposition can slow (Lorenzo *et al.* 2014). Consequently, reduced availability of nutrients to plants could limit their growth (Frouz 2018; Frouz *et al.* 2015).

It could be expected that decomposition rates and decomposer invertebrate communities would show parallel responses to the large environmental changes involved in both deforestation and any subsequent vegetation recovery. However, Ewers *et al.* (2015) found that logging of rainforest caused decomposition rates to increase relative to values in old-growth forest, despite a decrease in abundances of key functional groups of termites, ants, beetles and earthworms. Furthermore, Didham *et al.* (1998) found that fragmentation and habitat loss decreased decomposition rates, but with no apparent correlation between litter invertebrate abundances and litter decomposition rates. Such potential differences in patterns

of impact between decomposition rates and decomposer invertebrates highlight the importance of assessing both simultaneously, yet few studies have done so. Furthermore, no previous studies have investigated how both decomposition rates and communities of litter-dwelling invertebrate decomposers respond to the return of woody vegetation on disused pastures.

Here we evaluate the effects of forest-to-pasture conversion, and of subsequent forest restoration, on both decomposition rates and communities of litter-dwelling invertebrate decomposers, across multiple sites in a subtropical rainforest landscape. We also assess the correspondence between decomposition rates and decomposer abundances, and the effect of excluding macro-invertebrates ($> 1\text{ mm}$) from decomposing litter. We focus on the following question: how do deforestation for pasture and subsequent pathways of regeneration (both assisted and unassisted) affect the facilitation of litter decomposition rates by litter invertebrate communities?

METHODS

STUDY REGION- The study was conducted within the Numinbah Conservation Area and surrounding Numinbah Valley in subtropical southeast Queensland, Australia, spanning approximately 6.5 km^2 ($28^{\circ}9'44''$ - $28^{\circ}9'48''$ S, $153^{\circ}13'30''$ - $153^{\circ}15'57''$ E). The typical climate comprises a mean annual rainfall of about 1,400 mm (with wet summers and dry winters) and mean annual temperatures of about 16-26 °C (BoM 2018). Prior to European settlement, the area was almost entirely forested, and supported an ecosystem mosaic comprising several types of rainforest (with highest tree diversity), interspersed with other

types of more open eucalypt-dominated forests, especially on steep slopes and ridges (S1; see also Sattler and Williams 1999).

Deforestation commenced with European settlement in the mid-1800's, during which time selective timber harvesting was soon followed by clear-felling and establishment of cropland and pasture, especially in low-lying rainforest areas (Hall *et al.* 1988). By the early 1900s, extensive pasture areas had been formed, using non-native grasses and legumes, for dairy and beef production, leaving forest remnants in less accessible areas and on steep slopes (Hall *et al.* 1988). Many pastures were either subsequently abandoned as the dairy industry declined from the mid to late 1900s, and were gradually replaced with self-organised (natural) woody regrowth, but some pastures still remained into the 2000s.

At the time of the present study, the woody vegetation types were a mix of old-growth forest (both rainforest and eucalypt forest) unmanaged successional (regrowth) vegetation, and areas of this regrowth which additionally had been targeted for assisted natural regeneration (ANR) during the previous decade, by the managers of the Numinbah Conservation Area.

The unmanaged regrowth was characterised by relatively short trees and shrubs that provided a sparse canopy cover, with a high proportion of non-native species, most notably the shrub *Lantana camara* (Uebel *et al.* 2017). The ANR interventions aimed to accelerate regeneration of native trees, mainly by suppressing *L. camara* and other non-native plants using various cutting and herbicide applications, until seedlings and saplings of native trees had grown to close the canopy (Uebel *et al.* 2017).

STUDY DESIGN- We used a mixture of observational and manipulative experiment to assess how invertebrate-mediated leaf litter decomposition was affected by conversion of rainforest

to pasture, and during two pathways of vegetation recovery. In a space-for-time approach, we selected five vegetation types (Fig. 1), with five sites in each (S1.A). First, the two reference states of old-growth rainforest and grazed pasture represented both the effect of vegetation conversion and the target of restoration. Second, there were three types of regenerating vegetation, all based on 20-50-year-old woody regrowth: unassisted natural regeneration (UA); ANR which had begun 1-3 years previously; and ANR which had begun 5-10 years previously. All sampling at each site took place within a circle of 7-8 m radius, but the surrounding vegetation was similar up to a radius of at least 100 m.

FIGURE 1 Schematic diagram showing typical vegetation structure, land-use history and vegetation age of the five vegetation types (each with 5 sites): F= forest; P= pasture; UA= unassisted natural regeneration; AR1= assisted natural regeneration (ANR) 1-3 yrs; AR2=

ANR 5-10 yrs. Arrows indicate time and the length of time is shown in years (yrs).

Regenerating forest (Early regen, Woody regrowth and UA) was often dominated by invasive non-native lantana (*Lantana camara*) thickets which are indicated by the grey shaded vegetation. The cattle exclusion symbols indicate the vegetation types (UA, AR1 and AR2) where cattle have been excluded for at least five years. The lantana exclusion symbols indicate vegetation types (AR1 and AR2) where non-native species have been removed, followed with continued suppression of their growth.

Pasture areas had a dense cover of short grazed pasture species (mainly grasses) and contained very few trees. Rainforest reference areas had a dense shady canopy of medium to tall trees (>20 m) of many species and plant families (see also S1), multilayered foliage, and a thick layer of ground litter. UA sites had patches of shady canopies of medium trees (mostly <20 m), wide open canopy gaps usually filled with the non-native shrub *L. Camara*, and varied thickness of layers of ground litter. ANR sites aged 1-3 years had sparse canopy cover and medium trees (mostly <20 m), wide open canopy gaps filled with thick layers of killed *L. Camara* mulch, seedlings and saplings of mostly native pioneer rainforest species, and scattered low to moderate layers of ground litter. ANR sites aged 5-10 years had largely continuous canopy coverage of many thin stemmed medium trees (mostly <20 m) and a moderate layer of ground litter.

Sites were selected with reference to specific criteria (below), with reference to: maps of pre-clearing vegetation types (Fig. S1.A (B)); historical aerial photography from years 1930, 1961, 1993, 1998, 2005, 2009, 2011, 2013 and 2016 to calculate age of woody regrowth (Fig. S1.B); maps of years commenced for all ANR areas (Fig. S1.A (C)); and site suitability was

confirmed by ground truthing. The site selection criteria for each vegetation type were based on differing chronological sequences of historical land-use (Fig. 1, S1), as follows. All sites were at 150-460 m elevation, on igneous rock substrates, and where pre-European vegetation was rainforest classified as Regional Ecosystem 12.8.3 (complex notophyll vine forest, Sattler and Williams 1999); all were at least 100 m apart, and at least 30 m from the edge of a different vegetation type. Forest sites were never cleared. All other sites had been completely deforested and used for pasture for 30+ years. All regenerating sites supported woody regrowth vegetation 20-50 years old, in which livestock had been excluded for at least five years. The two ANR vegetation types additionally had been subject to assisted regeneration interventions, which began either 1-3 years or 5-10 years prior to this study.

LEAF LITTER DECOMPOSITION- In each of the 25 sites we deployed eight, 25 x 25 cm, nylon mesh litter bags (mesh size 1 mm). Each bag contained leaves of five local tree species common in the study area, but collected from trees outside it in a mature, undamaged condition, one month prior to the experiment. The selected species represented a mix of soft and firm leaves and the pioneer, mid and late successional stages of regeneration: *Toona ciliata*, *Ficus macrophylla*, *Macaranga tanarius*, *Castanospermum australe*, and *Acacia disparrima*. Leaves of all species except *A. disparrima* were cut into 2 x 3 cm pieces to standardise leaf weight and size, and then oven-dried at 50 °C until constant weight, thereby obtaining dry weights of about 0.02 g per leaf-piece. About 4 g of each species was then placed into each bag, totalling about 20 g per bag. We also perforated half of the bags (100 of 200) by making 12, 1-2 cm cuts, six into each side. For each site, this gave four open bags (which allowed access by all sizes of invertebrate) and four closed bags (which excluded macro-invertebrates due to the 1 mm mesh size).

All bags were placed in the field in December 2016, attached to the ground surface with metal pegs, in pairs (one open, one closed, 1 m apart), with the four pairs spaced 10 m apart around the 7-8 m radius circle. Over each pasture bag, we anchored a cover of arched wire 10 x 10 cm mesh, to protect it from livestock. Two pairs of bags (two open, two closed bags) were retrieved from each site after five months (155 +/-8 days), with the remaining two pairs retrieved at eight months (248 +/-7 days), and were all placed into individual plastic bags during transportation. We cleaned the leaves of soil and debris with water, oven-dried them at 50°C until constant weight, and then calculated the percent of original dry mass lost per bag. We also recorded the condition of each bag as: closed, open, or closed/open (due to additional holes created in closed bags during deployment).

INVERTEBRATE SAMPLING- To sample the ambient litter invertebrate community around the bags, we hand-collected a single 1 L litter sample from across the ground surface at each site, five months after litter bag deployment. These were transferred to the laboratory within a few hours of collection, and invertebrates were extracted over 72 hours using Tullgren funnels and collected in ethanol-filled jars.

Using a light microscope, we first grouped all invertebrates into two body size categories: macro (>1 mm long and wide) and meso (<1 mm long or wide) corresponding to the bag mesh size threshold. We also identified all to a level sufficiently fine to enable a dominant feeding guild (Stork 1987) to be assigned (for example, to Family for most beetles, to Infraorder for termites, to Class for centipedes); these guilds were decomposers (detritivores), predators, herbivores and fungivores. In some cases we chose the feeding guild known to be most common for a broader taxon. These data were then expressed as counts of individuals per site in each body size-feeding guild combination, at the Class or Order level.

DATA ANALYSES- All statistical analyses were conducted in R version 3.5.1 (R 2016). To investigate the effects of litter bag treatments, collection time and vegetation type on decomposition rate (mass loss %) we used linear mixed models (LMM) with Gaussian errors using ‘lmer’ in lme4 v1.1-21 (Bates *et al.* 2015), with bags as replicates. The initial total of 200 deployed litter bags was reduced, due to (1) 41 initially-closed bags that were excluded from data analyses due to perforation during deployment (14, 27 after five, eight months); and (2) six bags (two open, four closed) that could not be found at eight months.

We used maximum likelihood ratio tests to determine the significance of interactions between predictor variables by comparing models with and without an interaction term, and the significance of bag treatment and collection time on mass loss by comparing models with and without each predictor. First, we included all bags (N= 157) to test the interactions between bag treatment (open, closed) and vegetation type (five types). Second, we used only open bags (N= 98) to test the interaction between collection time (5, 8 months) and vegetation type. Third, to test the effect of vegetation type on mass loss, we used open bags at five months (N= 50) to compare a full model with vegetation type as the only predictor to a null model with no predictor.

To investigate the effect of vegetation type on the abundances of macro- and meso-decomposers, with sites as replicates (N= 25), we conducted generalised linear mixed effect models (GLMM) using ‘glmer’ in lme4 with a Poisson error distribution and log-link. We used maximum likelihood ratio tests to test the effect of vegetation type on both macro- and meso-decomposer abundance, by comparing models with vegetation type as the only predictor to null models with no predictor.

For all LMM and GLMM's we also compared the fit between models by Akaike Information Criterion (AIC) and Bayesian Information Criterion (BIC) using maximum likelihood (Nakagawa and Schielzeth 2013). We also calculated the proportion of variance explained by fixed effects ($R^2_{\text{GLMM}(m)}$) and proportion of variance explained by both fixed and random factors ($R^2_{\text{GLMM}(c)}$) using the Nakagawa and Schielzeth (2013) method and 'r.squaredGLMM' function in MuMIn v1.43.6 (Bartoń 2019). All models were assigned site as both a random factor and the subject-level term, and all models were checked for homogeneity of variances and normality of residuals. For post-hoc pairwise testing between vegetation types we used Tukey tests with Bonferroni-Holm corrections using 'glht' in multcomp v1.4-10 (Hothorn *et al.* 2008). Graphs were plotted using ggplot2 v3.1.1 (Wickham 2016).

To test the strength of association between decomposers and decomposition rates, we calculated Pearson's correlations between mass loss percent after five months in open bags (averaged for each site) and the abundances of both macro- and meso-decomposers, both across all sites (N= 25), and across all non-pasture sites (N= 20).

Variation across sites in broad taxonomic composition (at Class and Order levels, depending on taxon) of macro- and meso-decomposers was visualised with non-metric multidimensional ordinations (NMDS). These were based on seven taxa and 23 sites for macro-decomposers (two pasture sites had no macro-decomposers) and 11 taxa and 25 sites for meso-decomposers and were run using 'metaMDS' from vegan v2.5-4 (Oksanen *et al.* 2018), with $\log(x+1)$ transformed data and Bray-Curtis inter-site dissimilarities. To identify which taxa contributed most strongly to the ordination patterns we added biplot vector overlays using the

‘envfit’ function in vegan. To test whether the composition of both macro- and meso-decomposers differed significantly among vegetation types we used analyses of similarity (ANOSIM) with 9999 permutations using ‘anosim’ in vegan, with and without pasture sites.

RESULTS

DECOMPOSITION RATES- There were no statistically significant interactions in the effect on decomposition rates (mass loss %) of either bag treatment or collection time (Tables S2.A, S2.B). Decomposition rates increased from five to eight months (Fig. S2; likelihood ratio test $P=0.03$; Tables S2.A, S2.B), but were only 2.4 % greater at eight than five months.

Exclusion of macro-invertebrates using closed litter bags reduced the rate of decomposition by 3.1 % (likelihood ratio test $P=0.02$; Tables S2.A, S2.B). Using AIC and BIC criteria, the model with best fit used vegetation type as the only predictor of mass loss (Table S2.A).

Henceforth we concentrate on how vegetation type affected results from open litter bags at five months, because this time encompassed the period of greatest litter mass loss and is most likely to reflect decomposition rates mediated by the full suite of decomposers including macro-invertebrates. After five months of bag exposure, vegetation type had a strong effect on decomposition rates in open bags, which were almost 50 % lower in anthropogenic pasture than in forest (Fig. 2; likelihood ratio test $P<0.0001$; Tables S2.A, S2.B, S2.C). All types of regenerating vegetation showed considerable recovery (with decomposition rates being about 83 % of those in forest); but all nevertheless remained significantly lower than forest values and were not significantly different from one another (Fig. 2; Table S2.C).

FIGURE 2 Means and SEs of litter decomposition rates (mass loss % after 5 months) across five vegetation types representing different stages of deforestation for pasture and subsequent regeneration (vegetation type names as in Fig. 1; $N = 5$ sites in each). Mass loss percent was averaged across two open litter bags per site. Means with the same letter are not significantly different ($P > 0.05$).

DECOMPOSER ABUNDANCE- Ambient surface litter samples collected five months after litter bag deployment yielded 280 macro- and 6191 individual meso-invertebrates in total, across all feeding guilds (Table 1); decomposers were the most abundant guild across all invertebrates (53 % of 6,471) followed by predators (41 %), fungivores (4 %) and herbivores (2 %). The most abundant taxa among macro-decomposers were Amphipoda, Isopoda and Diptera larvae, and among meso-decomposers were Collembola, Amphipoda, Isopoda, Diptera larvae and Coleoptera.

TABLE 1. Counts by vegetation type of macro and meso invertebrate decomposer (detritivore) taxa and other functional groups sampled from 25 x 1 L ambient leaf litter at five months post litterbag deployment. Macro = >1mm long and wide, meso = <1mm long and wide. O – Order, C – Class, IO – Infraorder.

Higher taxa	Decomposer taxa	Taxonomic level	Macro										Meso			
			Macro	Meso	Total	Pasture	Unassisted	ANR 1-3yrs	ANR 5-10yrs	Forest	Pasture	Unassisted	ANR 1-3yrs	ANR 5-10yrs	Forest	
Annelida	Megadrilacea	O	0	28	28	0	8	11	20	33	17	3	2	1	5	
Myriapoda	Symphyla	C	0	57	57	0	0	0	0	0	0	8	19	1	29	
	Diplopoda	C	10	138	148	0	4	1	0	5	1	40	29	11	57	
Crustacea	Amphipoda	O	72	464	536	0	0	0	0	0	0	84	80	74	226	
	Isopoda	O	51	304	355	0	12	13	18	8	4	78	68	72	82	
Entognatha	Collembola	O	1	1490	1491	0	0	0	1	0	152	382	363	304	289	
Insecta	Diptera larva	O	45	283	328	1	15	14	11	4	14	71	132	25	44	
	Termitoidea	IO	0	6	6	0	0	0	0	0	0	0	1	0	5	
	Blattodea	O	24	14	38	0	10	3	5	6	0	5	2	2	5	
	Lepidoptera larva	O	24	90	114	0	0	0	3	19	0	0	5	0	9	
	Coleoptera	O	23	23	46	23	23	23	23	23	23	23	23	23	23	
Decomposers all	-	-	250	3171	3421	3	53	47	66	80	196	725	773	526	874	
Predators all ¹	Mixed	-	23	2646	2669	-	-	-	-	-	-	-	-	-	-	
Herbivores all ¹	Mixed	-	5	142	147	-	-	-	-	-	-	-	-	-	-	
Fungivores all ¹	Mixed	-	2	232	234	-	-	-	-	-	-	-	-	-	-	
	Overall total		280	6191	6471		-	-	-	-	-	-	-	-	-	

¹ Predators consist of Nematoda, Annelida, Entognatha, Onychophora, Myriapoda, Arachnida and Insecta. Herbivores consist of Mollusca and Insecta. Fungivores consist of Entognatha and Insecta.

Vegetation type had a strong effect on the abundances of both macro- and meso-decomposers, because both were about 95 % less abundant in anthropogenic pasture than in forest (Fig.3; likelihood ratio tests, $P = <0.0001$, $P = 0.0002$ respectively; Table S3.A, B, C, D). However, in all types of regenerating vegetation, abundances of both macro- and meso-decomposers had recovered to levels that did not differ significantly from forest values, and vegetation types were not significantly different from one another (Fig.3; Tables S3.C, D).

FIGURE 3 Means and SEs of abundances of (A) macro- and (B) meso-decomposer invertebrates (body length and width threshold 1 mm) extracted from litter samples, across five vegetation types representing different stages of deforestation for pasture and subsequent regeneration (vegetation type names as in Fig. 1; $N = 5$ sites in each). Means with the same letter are not significantly different ($P > 0.05$).

Across all sites, abundances of both macro- and meso-decomposers had strong positive correlations with decomposition rates (Fig. 4; respectively $r = 0.68$, $P = 0.0002$ and $r = 0.70$, $P = 0.0001$; $N = 25$ sites). However, when pasture sites were excluded this relationship weakened greatly, becoming non-significant for macro-decomposers ($r = 0.34$, $P = 0.17$; $N = 20$ sites), but was still significant for meso-decomposers ($r = 0.47$, $P = 0.04$; $N = 20$ sites).

FIGURE 4 Relationships between litter decomposition rates (mass loss % after 5 months, in open bags) and abundance of (A) macro and (B) meso decomposer invertebrates (body length and width threshold 1 mm) extracted from litter samples, across $N = 25$ sites representing different stages of deforestation for pasture and subsequent regeneration. Without pasture sites, respective r values were 0.34 ($P = 0.17$) and 0.47 ($P = 0.04$), $N = 20$ sites. “Regen.” are the regenerating vegetation types. Vegetation type names as in Figure 1.

DECOMPOSER COMPOSITION- NMDS ordinations showing the pattern of similarities among all sites according to their broad taxonomic composition revealed clear separation between sites in pasture and those in all other vegetation types (Fig. 5). This was supported by ANOSIM where differences in decomposer composition among vegetation types were marginally significant for macro- (Global $R=0.12$, $P=0.05$) and strongly significant for meso-decomposers (Global $R=0.36$, $P=0.001$) (Table S4). However, these differences disappeared, when pasture sites were excluded, for both macro- and meso-decomposers (Global $R=-0.07$, $P=0.82$; Global $R=0.09$, $P=0.10$ respectively; Table S4).

FIGURE 5 NMDS ordinations showing among-site variation in broad taxonomic composition (Order/Class level) of (A) macro- and (B) meso-decomposer invertebrates (body length and width threshold 1 mm) extracted from litter samples. There were seven macro-decomposer taxa present across 23 sites and 11 meso-decomposer taxa present across 25 sites. Different symbols show different stages of deforestation for pasture and subsequent regeneration (Regen.; all vegetation type names as in Fig. 1).

Biplot vector overlays for both macro- and meso-decomposers showed that most taxa were associated with the region of the ordination plot which contained both forest sites and all types of regenerating vegetation; the only taxa tending to associate with pasture sites were Coleoptera (beetles) among macro-decomposers, and Megadrilacea (earthworms) among meso-decomposers (Fig. S4).

DISCUSSION

THE EFFECT OF MACRO-INVERTEBRATE EXCLUSION AND EXPOSURE DURATION ON DECOMPOSITION RATES- Macro-invertebrates increased decomposition rates, but their exclusion lowered the rate of mass loss by only 3.1 %; much less than an average of 50 % reduction in decomposition rates reported in a multi-site tropical litter bag study conducted in rainforests over several countries (Powers et al. 2009). Different litter bag exposure durations could affect mass loss. However, the eight-month duration in our study was similar to the nine months of Powers et al. (2009). They compared mass loss between litter bags with mesh sizes of 0.05 mm and 2.0 mm so the results of their study reflect in part the effect of excluding invertebrates of body size 0.05-1 mm (i.e. some meso invertebrates), as well as some macro invertebrates (1-2 mm). This finding suggests that small invertebrates <1 mm may play a significant role in rainforest ecosystems.

The above suggestion is consistent with our finding that decomposition rates in open bags were more strongly correlated with abundances of meso-decomposers (< 1 mm) in surrounding leaf litter than of macro-decomposers. In our rainforest region, where this study deployed 1.0 mm mesh bags during a hot, moist subtropical summer, further research incorporating a smaller mesh size could potentially reveal larger effects on decomposition

rates. However, fine mesh bag sizes (<1 mm) can alter microclimatic conditions, leading to reduced decomposition rates (Bradford *et al.* 2002). Therefore the 0.05 mm mesh exclusion bags in Powers *et al.* (2009) may have overestimated the magnitude of the effect of meso-invertebrates on decomposition, and it would remain a challenge to distinguish the relative role of potential bag effects in future research.

Our results for open versus closed litter bags broadly resemble those of the tropical rainforest study by Cuke and Srivastava (2016), who found that the exclusion of macro-invertebrates (using 1.0 mm mesh) decreased decomposition rates by 7-16 % compared with bags which allowed access by larger decomposers through a 9 mm mesh. Cutting several access holes into the 1mm mesh as we did and using a larger mesh size are both common techniques to allow access by larger invertebrates. The slightly greater magnitude of macro-invertebrate effect on decomposition reported by Cuke and Srivastava (2016) could be either because the 9 mm mesh bags better enabled macro-invertebrate access, or because their larger mesh size allowed more fine litter to fall out during handling.

Leaves exposed in open bags for eight months in our study's forest sites had lost 79.3 % of their initial dry mass, and this litter decomposition rate is consistent with the rate of about 80 % reported from other tropical forests (Hättenschwiler *et al.* 2011). However, after five months, that review (Hättenschwiler *et al.* 2011) reported decomposition rates of about 50 %, compared with the 79.1 % found in our study, indicating that decomposition occurred relatively rapidly during our warm, moist study period. Using a shorter litter bag deployment duration in our study region could reveal early-phase dynamics of decomposition in which macro-invertebrates make a greater contribution to decomposition rates, in old-growth forest.

THE EFFECT OF CONVERTING FOREST TO PASTURE ON DECOMPOSITION RATES AND

INVERTEBRATE DECOMPOSERS—Decomposition rates have been shown by several previous studies to be greatly reduced when tropical forests are converted to anthropogenic pasture or agricultural use (Lorenzo et al. 2014; Szefer et al. 2017; Paudel et al. 2015). Our study similarly revealed reduced decomposition rates in anthropogenic pasture compared to forest. Equal decomposition rates in anthropogenic pasture compared with forest have occasionally been reported (Lorenzo et al. 2014). But this could be explained by a low decomposability of the chosen leaf substrate (e.g. high C:N ratio, lignin content) and an exposure time too short (90 days) to detect a difference. Differences in decomposition rates are also likely to be strongly driven by changes in physical habitat structure such as loss of canopy cover and greatly reduced litter fall, both of which contribute to the humid and shady microclimates which facilitate high rates of decomposition (Grimbacher and Catterall 2007; Nakamura *et al.* 2003).

Our results also show that deforestation for development of anthropogenic pasture had a strongly negative effect on communities of invertebrate decomposers. Irrespective of body size, decomposer abundance was greatly reduced in pasture. Further, we also found altered taxonomic composition of decomposers in pasture compared with forest, driven by concurrently reduced abundances across most decomposer taxa. The few similar studies which have assessed the impact of this land use change on the abundance of litter dwelling invertebrates (not necessarily decomposers), sometimes within specific taxa, have mainly also showed a large decline in abundance. For example, Nakamura *et al.* (2008) found a strong decrease in the abundance of litter dwelling invertebrates including centipedes, millipedes, isopods and amphipods, which occurred irrespective of body size. In cases where abundances were found to be higher in pasture than forest, this could often be explained by a

narrow taxonomic focus, for example Gove *et al.* (2005) found that ant abundance increased in pasture compared with forest, but ants are not *in situ* litter decomposers.

RECOVERY OF DECOMPOSITION RATES AND INVERTEBRATE DECOMPOSERS- Across all types of regenerating vegetation sites in our study, within 20-50 years since regeneration began on former pasture, decomposition rates had returned to about 80 % of those in forest rates and communities of litter decomposers had fully recovered in terms of both total abundance and broad taxonomic composition (at Class/Order level). This is broadly consistent with the suggestion that re-establishment of a more forest-like vegetation structure (and associated abiotic conditions) facilitates recovery of invertebrate decomposers and, in turn, of higher decomposition rates (Grimbacher and Catterall 2007; Nakamura *et al.* 2003), irrespective of floristic composition.

Few studies have simultaneously quantified both the reduction of decomposition rates of tree-derived leaves following conversion of forest to pasture, and their extent of recovery towards reference forest values following forest restoration (Table 2). For litter invertebrates (not necessarily decomposers), the limited previous research into recovery during forest regeneration has yielded highly variable findings (Table 2). This variability is likely due to wide variation in factors that affect invertebrate communities and their measurement, such as restoration age and technique, vegetation quality, focal invertebrate taxon and level of taxonomic resolution, invertebrate dispersal capacities and proximity to intact reference forest. All sites in our study were near large areas of intact forest, hence dispersal of invertebrate decomposers into the regenerating sites was unlikely to be a limiting factor, and our study had a broad taxonomic focus, allowing for the possibility that different species in restored versus forest sites may nevertheless have similar ecosystem functions.

TABLE 2. Review of the recovery of decomposition rates (mass loss) and abundance of litter dwelling invertebrates in the tropics and subtropics. Studies were included if they were in English, forested ecosystems, had passive and/or active restoration together with a forest reference. The decomposition rate studies all used litter bags filled with the same leaf species across all vegetation types within each study to measure dry mass loss (%). D decreased, I increased, S same (no change), P partial, Y recovered, N not recovered, * uncertain due to absence of agricultural reference, - not applicable.

Paper No.	Original forest type	Country	Agricultural use (No. years if known)	Passive restoration age	Active restoration age/duration (years)	Forest to pasture conversion		Recovery with passive restoration		Active restoration	
						Decomp. Rate	Invert. Abund.	Decomp. Rate	Invert. Abund.	Decomp. Rate	Invert. Abund.
1	Rainforest	Australia	Pasture (30+)	20-50	1-10	D	D ^a	P	Y ^a	P	P ^a
2	Rainforest	Brazil	Pasture (4)	20	-	D & S	-	Y	-	-	-
3	Rainforest	New Guinea	Slash & burn agri. (1-3)	5	-	D	-	Y	-	-	-
4	Rainforest	China	Slash & burn agri.	Unknown	-	D	-	Y ²	-	-	-
5	Rainforest	Brazil	Slash & burn agri. (20)	14-19	-	-	-	Y	-	-	-
6	Dry forest	Mexico	Slash & burn agri.	3	-	-	-	P*	-	-	-
6	Dry forest	Mexico	Slash & burn agri.	13	-	-	-	Y	-	-	-
7	Rainforest	Guatemala	Crops	1	-	-	-	P*	-	-	-
7	Rainforest	Guatemala	Crops	3-14	-	-	-	Y	-	-	-
8	Forest	Argentina	Crops	20	-	-	-	Y ³	-	-	-
9	Rainforest	Puerto Rico	Pasture	10-80	-	-	-	P*	-	-	-
10	Rainforest	Brazil	Pasture (4)	10-17	-	-	-	Y	-	-	-
11	Rainforest	Mexico	Unknown	35	-	-	-	Y	N ^a	-	-
12	Dry forest	Mexico	Pasture/agriculture	Unknown	-	-	I ^b	-	P ^b	-	-
13	Rainforest	Costa Rica	Crops?	Unknown	-	-	-	-	P* ^a	-	-
14	Rainforest	Australia	Pasture	20-40	-	-	D ^b	-	P ^b	-	-
15	Rainforest	Australia	Pasture	30-40	-	-	D ^c	-	P* ^c	-	-

16	Rainforest	Australia	Pasture	-	-	-	D ^a	-	-	-	-
17	Rainforest	Australia	Pasture	-	-	-	D ^c	-	-	-	-

Paper No. authors: (1) this study; (2) Lorenzo et al. 2014; (3) Szefer et al. 2017; (4) Paudel et al. (2015); (5) Barlow et al. 2007; (6) Xuluc-

Tolosa et al. 2003; (7) Ewel 1976; (8) Mendoza 2017; (9) Ostertag et al. 2008; (10) Vasconcelos & Lawrence 2005; (11) Barajas-Guzman &

Alvarez-Sanchez 2003; (12) Gove et al. 2005; (13) Cole et al. 2016; (14) Piper et al. 2009; (15) Grimbacher et al. 2006; (16) Nakamura et al.

2003; (17) Grimbacher & Catterall 2007.

¹Assisted natural regeneration (ANR)

² Except for one leaf species first deployed in the dryer months

³Except for one leaf species

^aVarious invertebrate Orders and Classes

^bAnts; abundance increased in pasture compared with forest, and intermediate abundance in regrowth c indicated partial recovery.

^cBeetles

Previous studies comparing the outcomes of different techniques of vegetation restoration for both decomposition rates and decomposer communities are almost entirely lacking (Table 2). Two meta-analyses have made broad indirect comparisons between separate studies of passive and active restoration (albeit with different techniques often studied in different regions) which have measured a range of variables, including indicators of decomposition processes (such as carbon, nitrogen, phosphorus) as well as various types of invertebrates (Crouzeilles *et al.* 2017; Meli *et al.* 2017). Overall, both reviews concluded that the available evidence did not support the notion that actively restoring former agricultural land (primarily by planting trees) achieved greater restoration success than could be obtained through natural regeneration. However, these analyses were broad-scale and could not account for many uncontrolled variables, and few of the reviewed studies had examined the outcomes of ANR. Nevertheless, the lack of difference in outcomes of passive and active restoration in our study was consistent with these suggestions.

Uebel *et al.* (2017) found that ANR accelerated the early recovery of physical vegetation structure in the same study location as our study. However, we found no effect of differing age of ANR sites (1-3 versus 5-10 years) on the return of either decomposition rates or invertebrate decomposer communities. This suggests that both these attributes had likely recovered from their low values in pasture to the levels measured in regenerating sites earlier, before our different types of regenerating site had diverged from one another (Fig. 1), and that any immediate impacts of herbicide treatments and associated short-term canopy foliage reduction in the younger (1-3 year) ANR sites must have been transient. In contrast to our finding for decomposition rates, Aragón *et al.* (2014) found significantly higher decomposition following ANR-like interventions (removal of non-native plant species)

compared with vegetation in which abundant non-native plants were retained, in a litter bag study of montane sub-tropical forest regrowth of similar age to our study (30-50 years).

Despite some inconsistency between the partial recovery in regenerating sites of decomposition rates, compared with the full recovery of both invertebrate decomposer abundances, there was a strong positive relationship between decomposition rates and the abundances of both macro- and meso-decomposers, across the full vegetation spectrum from pasture through regenerating sites to forest, and for meso-decomposers this correlation also remained when pasture sites were removed. These findings point to a strong functional role for meso-decomposer invertebrates during the restoration of rainforest to former pasture areas.

CONCLUSIONS- Our study shows a relatively rapid partial recovery during rainforest restoration, of both decomposition rates and communities of decomposer invertebrates, both of which had likely occurred prior to woody regrowth reaching 20-50 years of age. However, meaningful comparisons between these findings and those of other studies were difficult, because the designs of most studies did not include reference states of both agricultural land and forest, and because of large among-study variations in the age and type of revegetation, environmental context and measurement methods. These problems stem in part from a lack of a well-defined paradigm within which to consider recovery of the decomposition function (encompassing decomposition rates, decomposer organisms and associated ecological factors), when forest cover returns after once-forested land has been used for agriculture. Importantly, for studies to determine recovery patterns of any ecosystem process following deforestation and vegetation conversion, it is necessary to include both converted (e.g., agricultural, pasture) and forest reference conditions into their designs. Future generalisations

would also benefit from better standardisations of methods across a wide array of sites.

Ecosystem processes then need to be compared between converted and regenerating states to determine how much recovery has been made, and between regenerating and reference forest to determine how much more recovery remains before mature forest conditions are recovered.

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DATA AVAILABILITY STATEMENT

Data Availability: The data used in this study are archived at the Dryad Digital Repository (<http://dx.doi.org/10.5061/dryad.35p39r6>)

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SUPPLEMENTARY INFORMATION

S1 Description of original vegetation and aerial photos of the study area.

S2 Extra results of decomposition rates (LMM's, likelihood ratio tests and post-hoc results) and example R script for decomposition rates.

S3 Extra results of decomposer abundance (GLMM, likelihood ratio tests and post-hoc results), and example R script for decomposer abundance.

S4 Extra results of decomposer composition (data, ANOSIM and ordination biplot vectors) and example R script for decomposer composition.