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Leaf litter decomposition in tropical freshwater swamp forests is slower in swamp than non-swamp conditions

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ABSTRACT

Decomposition is a key ecosystem function, and the rate of decomposition in forests affects their carbon storage potentials. Processes and factors determining leaf litter decomposition rates in dry-land and temperate forests are well understood, but these are generally poorly studied in tropical wetland forests, especially freshwater swamp forests (FSF). The home-field advantage (HFA) hypothesis predicts that soil microbes specialize in decomposing leaf litter produced by the tree species in their immediate vicinity. However, empirical support for the HFA is equivocal, and the HFA has never been tested in the highly heterogeneous and biodiverse ecosystems of tropical FSFs. We collected leaf litter from swamp and non-swamp tree species in a tropical FSF in Singapore and monitored the decomposition rates of these in swamp and non-swamp plots for a period of eight months. Leaf litter decomposed 3.7 times more slowly in swamp plots. Leaf litter from swamp tree species were significantly poorer in quality (higher C:N ratio) than those of non-swamp FSF tree species, but this had only a weak effect on decomposition rates. There was also only weak evidence for the HFA and only in non-swamp conditions. Our results show that while the leaf litter of tropical FSF swamp and non-swamp tree species differ significantly in chemical traits, litter decomposition rate is ultimately determined by local abiotic conditions, such as hydrology. Additionally, the high FSF tree diversity may prevent decomposer communities from specializing on any group of leaf litter types and thus limit the extent of HFA observed in such heterogeneous forests.

KEYWORDS

carbon sequestration, C:N ratio, ecosystem process, home-field advantage, leaf litter quality, Southeast Asia, peat, waterlogged soil

1. INTRODUCTION

Decomposition is a key ecosystem function and is critical to the maintenance of the carbon cycle globally (Aerts 1997). The rate at which decomposition occurs in forests both determines the productivity and affects the carbon-sequestering ability of systems (Chapin *et al.* 2002). At the global scale, climate is one of the strongest determinants of leaf litter decomposition rate, with decomposition rates more rapid with higher actual evapotranspiration (Meentemeyer 1978, Aerts 1997). However, because decomposition rates in different forest types can differ greatly even within a single climatic zone (Elliott *et al.* 1993), the carbon storage/sequestration of forests may be poorly estimated if only climatic variables are considered. A key goal of decomposition studies is thus to determine how biotic and abiotic factors interact within specific forest communities to determine decomposition rates.

Leaf traits—particularly those associated with leaf litter quality—are also important predictors of decomposition rates, and are even more important determinants of decomposition rates than climate in environments that do not experience extreme temperature or drought stress (Meentemeyer 1978, Couˆteaux *et al.* 1995). Leaves with traits associated with low leaf litter quality (e.g., high C:N ratio, high lignin content) generally decompose more slowly because specialized enzymes are required to breakdown recalcitrant carbon forms in them (Gholz *et al.* 2000, Chapin *et al.* 2002, Freschet *et al.* 2012). Most of these studies have been conducted in well-drained or 'dry-land' forests, especially those of temperate regions. However, some studies have shown that hydrological conditions are likely to interact with litter quality to determine litter decomposition rates in waterlogged swamp forests. Yule and Gomez (2009) showed that the high quality leaf litter of a generalist non-swamp tree species, *Macaranga tanarius*, decomposed faster in pools as compared to on dry areas in tropical PSFs, but the low-quality leaf litter of the congeneric swamp specialist, *Macaranga pruinosa*, decomposed at similar rates in

4

49   pools and dry areas of the same habitat. However, such an interaction has remained poorly

50   studied.

51   For waterlogged habitats such as temperate peat bogs, coastal mangrove forests, and

52   tropical swamp forests, it is generally understood that burial within peat and/or submersion

53   below water table levels slows decomposition through anoxia and acidification (Laiho 2006).

54   The rate of accumulation of organic matter that is higher than the loss rate through

55   decomposition and runoff leads to the accumulation of a deep layer rich in organic matter known

56   as peat, and makes such habitats important sinks of below ground carbon (Chapin *et al.* 2002,

57   Moore & Basiliko 2006). The understanding that waterlogging retards decomposition rates is

58   gained from multiple observations, including that drained peat bogs emit large amounts of

59   carbon dioxide due to accelerated decomposition rates immediately post-draining (Silvola *et al.*

60   1996, Chimner & Cooper 2003, Clarkson *et al.* 2014). Also, buried leaf litter often decomposes

61   slower than leaf litter placed on exposed substrates (Moore *et al.* 2007, Straková *et al.* 2012,

62   Clarkson *et al.* 2014), and litter decomposes faster aerobically than anaerobically under

63   laboratory conditions (Bragazza *et al.* 2013). In addition, coastal wetlands store significantly

64   greater amounts of carbon ("blue carbon") per unit area than terrestrial forests (Mcleod *et al.*

65   2011). However, this seemingly intuitive understanding is not without problems. A significant

66   number of studies actually show that decomposition rates are not always slower in waterlogged

67   habitats than in climatically similar well-drained habitats (Moore & Basiliko 2006), and that, in

68   the long term, the drainage of peatlands can sometimes lead to *increased* carbon storage

69   (Minkkinen & Laine 1998, Minkkinen *et al.* 2002, Laiho 2006). Although anoxia and

70   acidification caused by submersion in waterlogged peat substrates generally reduce

71   decomposition rates, the complex interactions between litter quality, decomposer communities,

72 and environmental conditions such as substrate pH, temperature, nutrients, etc. make it

73 impossible to infer general patterns of decomposition across all types of waterlogged habitats

74 (Laiho 2006).

75   There exists a great diversity of swamp habitat subtypes around the globe (Junk *et al.*

76 2011) for which our knowledge of ecological processes such as decomposition remains

77 superficial. In the tropics, inland swamp forests can generally be categorised into one of two

78 types: peat swamp forests (PSF), or freshwater swamp forests (FSF). Both tropical PSFs and

79 FSFs occur on permanently waterlogged soils, and many tree species found in them (for which a

80 moderate degree of taxonomic overlap exists) display adaptations to anoxia and unstable

81 substrates (Corner 1978). However, PSFs are almost exclusively rain-fed (ombrogenous) and

82 thus highly nutrient-limited, whereas FSFs receive dissolved mineral nutrients from rivers and

83 streams, and are thus often nutrient-rich (Page *et al.* 2006, Chong *et al.* unpublished data).

84 Several studies have investigated decomposition rates in tropical PSFs (Yule & Gomez 2009,

85 Ong *et al.* 2017), but to the best of our knowledge, there are no published studies on

86 decomposition in tropical FSFs.

87   General patterns of decomposition are important for understanding the process of nutrient

88 cycling. However, the extrapolation of generalizations from the better studied systems of dry-

89 land forests, temperate and/or coastal mangrove peatlands to tropical inland swamp forests has

90 proven to be difficult (Yule & Gomez 2009, Bragazza *et al.* 2013), and differences between the

91 biogeochemical processes within each of these swamp habitat subtypes greatly limit the

92 transferability of findings between them (Laiho 2006). Even between tropical PSFs and FSFs,

93 despite many similarities in climate, vegetation physiognomy and biogeochemical properties,

94 differences in soil nutrient levels are still expected to limit the transferability of general patterns

of decomposition between the two forest types. Soil and/or substrate nutrient levels are known to interact with leaf litter quality to alter the decomposition rate of leaf litter (Freschet *et al.* 2012, Bonanomi *et al.* 2017). Soils of PSFs are very nutrient deficient (Page *et al.* 2006), and leaf litter quality of PSF species is often very low (Yule & Gomez 2009, Ong *et al.* 2015, 2017), but the soils of FSFs are often richer in nutrients (Chong *et al.* unpublished data), thus species which may produce higher-quality leaf litter. Hence, there is a need for studies of decomposition in FSFs, and a need for such studies to investigate the possible interactions between hydrological conditions and litter quality on decomposition rates.

Many studies in dry-land forests have also shown that leaf litter decomposition is faster when leaves decompose at the sites or habitats from which they originate—a phenomenon often referred to as the 'home field advantage' (HFA) (Gholz *et al.* 2000, Ayres, Steltzer, Berg, *et al.* 2009, Ayres, Steltzer, Simmons, *et al.* 2009, Gießelmann *et al.* 2011, Freschet *et al.* 2012, Yu *et al.* 2015, Gao *et al.* 2016, Sun & Zhao 2016). The likely reason for this is that soil microbes specialize in decomposing the mix of leaves produced by the plant communities at the site (Ayres, Steltzer, Berg, *et al.* 2009) and/or leaf litter that is most similar in chemical composition/quality to that of the leaf litter matrix (Freschet *et al.* 2012). Additionally, specialization in particular litter types may develop because both litter production and the decomposition abilities of soil microbes are constrained by local environmental conditions such as nutrient availability (Hoyos-Santillan *et al.* 2018). However, the HFA is not conclusively demonstrated in all well-drained forests (Gießelmann *et al.* 2011, Veen *et al.* 2015, Gao *et al.* 2016, Sun & Zhao 2016) and has not been tested extensively in waterlogged habitats. Hoyos-Santillan et al. (2018) found a strong HFA between a high-nutrient, palm-dominated area and a low-nutrient mixed forest area within a neotropical peat swamp forest, but Clarkson et al. (2014)

118   found no evidence of it between restiad peatlands of differing successional stages in New

119   Zealand.

120   In this study, we aimed to estimate the leaf litter decomposition rates within a catchment

121   containing a tropical freshwater swamp forest and to examine factors affecting these decay rates

122   to understand how leaf litter decomposition responds to different biotic and abiotic conditions of

123   this forest type. Tropical FSFs are spatially heterogeneous in hydrological and edaphic

124   conditions and are thus composed of sub-habitats and sub-communities that are typical of both

125   well-drained and waterlogged forests (Chong et al. unpublished data). To our knowledge, there

126   are no published studies on decomposition in tropical freshwater swamp forests. Our findings

127   may be useful for deducing how the ecology of this forest system may change under global

128   change. We tested the following hypotheses: (1) that there is a difference in leaf litter

129   decomposition rates between the well-drained (non-swamp) and waterlogged (swamp) areas

130   within tropical freshwater swamp forests; (2) that litter quality is a good predictor of

131   decomposition rates; and (3) that decomposition rates are affected by the home field advantage.

132   Hypothesis (1) tests the assumption that the submersion of leaf litter in water slows down

133   decomposition; hypothesis (2) tests whether factors other than litter quality are important in

134   determining decomposition rates of the swamp forests; and hypothesis (3) tests whether microbe

135   communities may be differentiated between swamp and non-swamp local site conditions and/or

136   specialize in decompose the leaf litter produced by trees in such conditions.

137

2. METHODS

1. Study areas

The study was conducted in ten 20 m × 20 m vegetation plots (Figure 1a) in the Nee Soon catchment in Singapore (1°23'27.3"N, 103°48'35.5"E). The Nee Soon catchment contains Singapore's last substantial, relatively intact tract of freshwater swamp forest (758 ha). Five of these plots (hereafter 'swamp plots') occurred in this swamp, with surface water within the plots, frequently waterlogged soil, and a water table that was no less than one meter below the soil surface level, while the remaining five plots (known hereafter as non-swamp plots) occurred in well-drained areas within the same catchment and did not have any surface water within them. The ten plots had been established earlier as a part of a larger study involving 40 plots and are used for the monitoring of forest tree communities in the Nee Soon freshwater swamp forest (Chong *et al.* 2016, 2018). They had been established through a random sampling procedure stratified between all available swamp-type and non-swamp-type areas within the watershed that constitutes the Nee Soon freshwater swamp forest. Tree communities in the five swamp and five non-swamp plots are clearly different (Figure 1b), and litterfall composition between them similarly reflect this difference (Lam et al. unpublished data).

2. Litterfall collection and processing

Litterfall was collected between September 2018 and June 2019 at fortnightly intervals from four 1 m × 1 m leaf litter traps established in each of these plots. Leaves collected from the five plots of each hydrological condition (swamp or non-swamp) were pooled, sorted by morphospecies, and thereafter dried for 7−21 days at room temperature in a box containing silica gel beads. At every collection, large numbers of species would be represented in litterfall (18.7 ±

161   12.1 [mean ± S.D.] species in non-swamp plots; and 14.8 ± 10.9 species in swamp; Lam et al.

162   unpublished data), but the bulk of the litter would be consistently and typically dominated by

163   species that were also dominant in the plant community within that hydrological condition. Leaf

164   litter was accumulated over multiple collections until enough litter was available for the

165   deployment of 60 leaf litter bags, i.e., six bags per plot (hereafter referred to as a "batch"). In

166   order to maintain compositional similarity between the litter bag contents for plots of the same

167   hydrological condition while ensuring that they preserved the diversity of leaf litter accumulating

168   with the different plot conditions, leaves of each morphospecies were distributed across all bags

169   within the batch, starting first with the most dominant litter morphospecies of each batch, until

170   the leaf litter in each bag had a combined mass of 6.00–7.00 g.

171   Litter bags were made from high-density polyethylene netting with 3-mm mesh size to

172   allow entry by mesofaunal detritivores, and measured 20 cm × 23 cm. They were sealed along

173   the edges of the bags using wax from a glue gun after leaves had been packed into them. Litter

174   bags were then randomly assigned to a hydrological condition (swamp or non-swamp) that was

175   either the same (the "home field") or different (the "away field") from the one from which they

176   had originated. They were tied to the legs of leaf litter traps using 1-meter long nylon strings for

177   ease of retrieval and left in the field for zero, one, two, four or eight months. A zero-month (i.e.,

178   immediate retrieval) time interval was used to control for potential leaf mass loss caused by

179   handling. A total of 560 litter bags (not including 108 litter bags which were deployed for zero-

180   month time intervals) were deployed, and were evenly distributed across plots, plot conditions,

181   and experimental durations.

182   Decomposition bags were deployed in batches between September 2018 and February

183   2020, and were planted such that replicates for the shorter-duration retrievals were deployed over

184   the whole period to control for potential effects of weather variations (but our study site, being in

185   the equatorial tropics, is considered relatively aseasonal). After retrieval, the contents of each

186   litter bag were washed and brushed gently over a 2-mm sieve to remove mud and other non-

187   organic debris. They were then dried in an oven at 60°C for six days before being weighed.

188

189   *3. Leaf chemical analyses*

190   To examine the effect of leaf litter quality on decomposition rates, and the possible

191   association between leaf litter quality and hydrological condition, elemental analyses were

192   performed on leaves from the zero-month time interval. Leaves were ground into fine powder

193   using a Rommelsbacher EGK 200 coffee grinder (Dinkelsbühl, Germany). Elemental carbon and

194   nitrogen composition of these powdered samples were then determined using a vario MICRO

195   cube elemental analyser (Elementar, Langenselbold, Germany), and the C:N ratio obtained from

196   this. Chemical analyses were performed on seven litter bags from each hydrological condition,

197   with six replicates for each litter bag, resulting in a total of 84 samples.

198

199   *4. Statistical analyses*

200   Leaf litter decomposition rate may be expressed as in Olson (1963) with slight

201   modification:

202
$$m_t = m_0(1 - l)\,e^{kt} \qquad\qquad (Eqn.\,1)$$

203   Where m_t is the dry mass of leaf litter at time t, the number of days that litter was left to

204   decompose in the field; m_0 is the initial mass at deployment; l is the proportion of mass lost due

205   to handling; k is the decay rate. Eqn. 1 may be linearized by taking the natural logarithm on both

206   sides:

$$\ln m_t = \ln(1 - l) + \ln m_0 + kt \qquad\qquad (Eqn.\,2)$$

208   Thus, k may be conveniently estimated when the log-transformed remaining dry weight of leaf

209   litter is regressed against the duration of field deployment with log-transformed m_0 as a

210   covariate. The log-transformed proportion of mass remaining after initial handling $(1 - l)$ is

211   therefore estimated as the intercept. Furthermore, it was possible to include additional variables

212   in such a model to estimate their potential effects on the rate of decay:

213
$$k \sim Plot_i + Origin_j + Plot_i \times Origin_j$$
$$\ln m_t \sim \ln m_0 + Plot_i \times t + Origin_j \times t + Plot_i \times Origin_j \times t \qquad (Eqn.\,3)$$

214   Where i and j indicate the plot type (swamp or non-swamp) in which decomposition occurred

215   and the origin of the litter (swamp or non-swamp species), respectively. The three-way

216   interaction $(Plot_i \times Origin_j \times t)$ is a first but not the only condition to determine if there is

217   HFA; HFA is considered to manifest if there is an increase in k when $i = j =$ swamp and/or $i =$

218    $j =$ non-swamp. Importantly, this definition of the HFA deviates from the conventional HFA

219   index (Ayres, Steltzer, Simmons, *et al.* 2009) by estimating potential asymmetry in the

220   phenomenon (e.g., litter of non-swamp species decompose faster in non-swamp conditions, but

221   litter of swamp species do not decompose faster in swamp conditions).

222   The model (Eqn. 3) was fitted using linear mixed-effects models with the R package

223   "*nlme*" (Pinheiro *et al.* 2019) and an exponential variance function. The exponential variance

224   function was chosen because the log-transformation of the original equation of decomposition

225   (Eqn. 1) results in errors which scale with remaining litter mass; thus, they are not normally

226   distributed (Adair *et al.* 2010). The litter batch and the plot where the bags were deployed were

227   included as crossed random effects in the model to account for potential non-independence for

228   the same batch or plot of deployment. Model selection was performed according to Burnham and

229   Anderson (2002) using the R package "*MuMIn*" (Bartoń 2016). All models were made to include

230   an intercept ($\ln(1 - l)$ in Eqn. 2) and the initial mass parameter ($\ln m_0$ in Eqns. 2 and 3) as

231   recommended by Adair et al. (2010). Sum of variable weights—that is, the sum of the Akaike

232   model weights of all models containing a given variable—were calculated for each variable as an

233   indicator of its importance relative to other variables. All statistical analyses were conducted in

234   the R v3.6.1 statistical programming environment (R Core Team 2018).

235   In order to visualize the data and examine the effect of litter origin on decomposition

236   while excluding the overwhelming effects of local site conditions resulting from plot type

237   differences, bootstrapping was performed on the proportion of remaining leaf litter over time.

238   We calculated the value of remaining litter proportion of non-swamp tree species minus that of

239   swamp tree species—a difference value which would be positive if litter from non-swamp tree

240   species decomposed more than that of swamp tree species, and negative if reversed. This value

241   was calculated for each batch of leaf litter, and resampled with replacement 9999 times within

242   each combination of plot type (swamp and non-swamp) and decomposition duration in months

243   (i.e., zero, one, two, four, or eight months). Bootstrapped medians and 95% confidence intervals

244   (CIs) were obtained from this sample.

245

3. RESULTS

Leaf litter decomposition in our experiments was well approximated by the exponential decay

function (Eqn. 1), with greater mass losses occurring earlier in experiments. All top (ΔAICc < 2)

models analysed had high R^2 values of approximately 73% (Table 1). Leaf litter also

decomposed much slower in swamp plots than in non-swamp ones. On average, leaves which

were left to decompose in swamp plots lost 47% of their dry mass by the end of eight months

(the longest experimental duration used in this study), but this value was approximately 80% for

leaves left to decompose in non-swamp plots.

Decomposition duration (i.e. time t in Eqn. 1), and the interaction between plot type and

decomposition duration were the most important predictors of remaining litter dry mass in

retrieved litter bags (Table 1; Fig 2). These two variables each had sum-of-weights values that

were close to 1 (Figure 2a) and strong estimated effects in all of the top models with ΔAICc < 2

(Table 1). Thus, the top three models all contained both these two terms—duration and its

interaction with plot type—while the remaining three models, which did not contain the

interaction term between duration and plot type, had negligible support from the data, with

model weights that were approximately zero (Table 1). We thus consider only the models ranked

first to third.

The first-ranked and most parsimonious model of remaining litter dry mass estimated the

coefficient of experimental duration to be −0.0066 (95% CI = [−0.0071, −0.0061]) in non-swamp

plots and −0.0018 (95% CI = [−0.0023, −0.0011]) in swamp plots. In other words, the

instantaneous rate of litter mass loss was 3.7× higher in non-swamp than swamp plots. The

model ranked second (ΔAICc = 0.456) contained the same variables as the first as well as the

interaction between experimental duration and leaf litter origin (Table 1). This model estimated

that leaf litter originating from swamp tree species decomposed 0.0004 day^{-1} more slowly on

270   average than litter originating from non-swamp tree species. The leaf litter origin ×

271   decomposition duration term had a sum-of-weights value of almost 60% (Figure 2a), indicating

272   some evidence in support for it as a predictor of remaining litter dry mass. However, the effect

273   was weak, with the bootstrapped 95% CI ranging from 0.0010 day^{-1} slower to 0.0002 day^{-1}

274   faster, i.e., 95% CIs intercepted with zero when decomposition duration and plot type were

275   controlled for (Figure 2c). Litter quality was evidently different between the types of leaf litter

276   origin, as C:N ratio of litterfall in swamp plots was found to be significantly higher than that in

277   non-swamp plots ($t_{82} = 17.9$, p-value < 0.001; Figure 3).

278   On the whole, there was only weak support for the HFA from the data. The model ranked

279   third ($\Delta AICc = 1.217$) was similar to the first two in all respects, albeit with slight differences in

280   parameter estimates, and the inclusion of the three-way interaction term between experimental

281   duration, leaf litter and plot type (Table 1) that is the first statistical condition of the HFA.

282   However, bootstrap median estimates of proportion of remaining litter of non-swamp tree versus

283   swamp tree species exhibited the expected hump-shape described by Ayres *et al*. (2009a) only

284   for non-swamp litter decomposing in non-swamp plots, albeit with confidence intervals both of

285   model coefficients and bootstrap estimates overlapping zeroes (Table1; Figure 2c). Leaf litter

286   originating from swamp tree species decomposed 0.0007 day^{-1} slower on average (95% CI =

287   [0.00, 0.16]) than litter originating from non-swamp tree species for leaf litter decomposing in

288   non-swamp plot types. When leaf litter decomposed in swamp plot types, the model estimated

289   that litter originating from non-swamp and swamp tree species decomposed at rates which are

290   approximately equal (Figure 2c).

291

292   **4. DISCUSSION**

293   In this study, we examined the decomposition of leaf litter from two groups of co-occurring but

294   functionally divergent tree species (swamp and non-swamp tree species) in contrasting local site

295   conditions (swamp and non-swamp conditions; Figure 1a) in the Nee Soon FSF in Singapore.

296   Decomposition rates in swamp plots were found to be much slower than decomposition rates in

297   non-swamp plots. C:N ratio of leaf litter shed by swamp tree species was also found to be

298   significantly higher (i.e., of a lower quality) than that of non-swamp tree species. But contrary to

299   expectation, there was only weak evidence to suggest that leaf litter origin affected

300   decomposition rate of litter, and that leaf litter originating from trees specialized to non-swamp

301   conditions decomposed faster in non-swamp conditions, i.e., the HFA. Taken together, these

302   findings suggest that, in FSFs, decomposition rates are overwhelmingly determined, not by traits

303   of the decomposing leaves or by the biotic effects associated with the HFA, but by abiotic—here,

304   hydrological–conditions at the sites of decomposition.

305   Decomposition is a key process in the global carbon cycle, which has been extensively

306   studied in well-drained forests and more recently in PSFs but remains unexplored in FSFs. We

307   show here that decomposition rates are highly dependent upon local hydrological conditions

308   within sites, with the most parsimonious model estimating decomposition rate (the k value of

309   Eqn. 1) to be 0.0066 day^{-1} in non-swamp conditions, and 0.0018 day^{-1} in swamp conditions, the

310   latter of which is very close to that estimated by Sulistiyanto (2005), Hoyos-Santillan et al.

311   (2015) and Yule & Gomez (2009) in PSFs. Our findings agree with the general observation that

312   buried or submerged leaf litter in swamps decompose slower than unsubmerged or more exposed

313   leaf litter (Moore *et al.* 2007, Straková *et al.* 2012, Clarkson *et al.* 2014). This observation

314   contrasts starkly with that which is observed in streams and riparian habitats, where submersion

315   often leads to higher decomposition rates (MacArthur et al., 1994; Nakajima et al., 2006; Junk &

316 Furch, 2014), possibly because streams are well-oxygenated in comparison to the anoxic

317 substrates of swamps. The findings of Yule & Gomez (2009) that leaf litter decomposes faster

318 submerged in pools than in the terrestrial environment of tropical PSFs are anomalous in this

319 regard, and may have been caused by unique local site effects. In our study, leaf litter bags from

320 non-swamp plots were often penetrated by plant roots, but this was never observed in leaf litter

321 bags from the swamp plots. It is likely that the mycorrhiza associated with these plant roots

322 would have accelerated decomposition in these litter bags from non-swamp plots. Flooding is

323 known to inhibit both fine root development and mycorrhiza proliferation (Kozlowski, 1997),

324 and this is one possible mechanism for the retardation of decomposition rate under swamp

325 conditions.

326 This information provided by our study also has crucial implications for the management

327 of tropical PSFs and FSFs. Surrounding land use changes (e.g., drainage for agricultural or urban

328 development) and climate change (e.g., decreased or irregular rainfall) can significantly alter

329 groundwater table depths in FSFs even while forest cover is retained. Our study shows that such

330 changes can result in more than threefold differences in the potential carbon loss rates from the

331 litterfall of such habitats. Thus, carbon monitoring programmes such as REDD+ must evaluate

332 the possibility of *hydrological* forest degradation when evaluating the state and carbon storage

333 potential of tropical forests (Mertz *et al.* 2012). Wetland habitats are increasingly being

334 recognized as globally-important carbon sinks, with slow decomposition rates being a common

335 attribute shared between these habitats and contributing to their ability to accumulate large

336 reservoirs of below ground organic matter (Mcleod *et al.* 2011, Lovelock & Duarte 2019, Iqbal

337 & Shang 2020).

338

339   *Litter quality and the home field advantage (HFA) in FSFs*

340   Our study also found only a weak effect of traits and HFA on litter decomposition in the

341   Nee Soon FSF in Singapore. Leaves with low C:N ratio contain high amounts of proteins and

342   nucleic acids (nitrogen-containing molecules) relative to the amount of structural tissues such as

343   lignin or cellulose (carbon-rich molecules, which do not contain nitrogen), and are thus

344   considered to be of a high quality. Studies of leaf litter decomposition in well-drained forests

345   have repeatedly shown that high quality leaves with low C:N ratios decompose faster than low

346   quality leaves with high C:N ratios (Aerts 1997). However, despite significant differences in C:N

347   ratios between leaf litter of swamp and non-swamp tree species (a finding which agrees with

348   those of Yule and Gomez [2009]), we found only a weak effect of leaf litter origin on

349   decomposition rates. Rather than a simple relationship between C:N ratio and decomposition

350   rate, we argue that other leaf traits such leaf chemistry (e.g., the presence and concentrations of

351   secondary metabolites (Chomel *et al.* 2016)) may interact with leaf C:N ratios to determine

352   decomposition rates (Ong *et al.* 2015, 2017). Given the varying ecophysiological stressors

353   affecting trees in dry-land forests, PSFs, and FSFs, and the effect that these stressors may have

354   on plant survival strategies, it seems unlikely that leaf C:N ratios alone may be used to predict

355   decomposition rates across diverse tropical forest types.

356   Regarding the HFA, our experiments found only very weak evidence supporting this and

357   only in terms of leaves from non-swamp tree species decomposing in non-swamp conditions.

358   Microbial communities are known to play important roles in the decomposition of leaf litter in

359   tropical swamp forests (Too et al., 2018), were likely to be the main agents of decomposition in

360   our experiments, given that macroinvertebrates had been excluded by the 3-mm mesh size of our

361   leaf litter bags. That a strong HFA was not observed thus suggests that litter-decomposing

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362   microbe communities do not segregate clearly between swamp and non-swamp areas in our

363   study site to specialize on breaking down the litters of only the tree species more abundant in

364   these respective areas. The simplest possible explanation for this observation is that the high

365   tropical plant diversity present even between plots sharing the same hydrological conditions

366   prevents decomposer communities from specializing on any group of leaf litter types. This

367   hypothesis is supported by the observation that non-swamp plots were more convergent in

368   canopy tree community composition than swamp plots (Figure 1b), and that the HFA was

369   therefore more evident—even if still extremely weak—in non-swamp conditions. If this is

370   indeed so, then our study suggests that, in highly diverse communities, the "home field" for

371   microbe decomposer communities occurs at the micro scale rather than at the plot or landscape

372   spatial scales. Unfortunately, the design of our study only permitted the testing of whether HFA

373   was observed or not, but did not allow for the testing of various mechanistic theories of the HFA.

374   For example, we neither examined the leaf litter matrix in which leaf litter bags were buried, nor

375   investigated the microbe communities responsible for early- or late-stage decomposition of the

376   litters.

377

378   *Limitations and future directions*

379   This study was conducted within the relatively small area of the Nee Soon FSF in

380   Singapore, and the extrapolation of our findings to all FSFs globally should thus be made with

381   caution. Differences in historical (e.g., legacies from exploitation), geographical (e.g.,

382   topography) and biological (e.g., tree species identities) may limit the generalizability of some

383   aspects of our study (e.g., the negligible HFA effect). Nevertheless, we argue that the main

384   finding of this study—that hydrological conditions are the main determinants of leaf litter

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385   decomposition in tropical FSFs—represents a phenomenon that is likely to be consistent across

386   all tropical FSFs because it is both pronounced in our study and brought about by the very

387   biochemical processes that define tropical FSFs.

388   Decomposition rates estimated using litter bag experiments often overestimate

389   decomposition rates slightly, because retrieval and washing of partially to extensively

390   decomposed leaves often result in the loss of small leaf fragments through litter bag meshes. Our

391   study suffers from a similar weakness, and it is thus possible that the k values reported here were

392   slightly higher than they are in reality. Nevertheless, the small mesh sizes (3 mm) used in our

393   study means that this overestimation is likely to be kept to a minimum, since most leaf fragments

394   in even the most extensively decomposed samples were still significantly larger than this. On the

395   other hand, the use of the 3-mm mesh effectively excludes many meso- and macro-detritivores,

396   such the reticulated swamp crab that is endemic to this catchment (Ng, 1990), which may play

397   important roles in the breakdown of litter especially in swamps and other freshwater habitats.

398   Finally, we used a simple exponential model which assumed constant proportional decay rates,

399   but the litter decomposition dynamics are more complex and more labile components would be

400   lost first (Grossman et al., 2020).

401   Local site abiotic (hydrological, edaphic and anoxic) conditions vary along a continuum,

402   as do the degrees to which tree species in FSFs specialize or associate with local site conditions

403   (Chong et al. unpublished data). However, we chose to describe both local site conditions and

404   leaf litter origins as binary variables: swamp versus non-swamp. Furthermore, leaf litter in this

405   study was too diverse to carry out a study of differences between species, and we were thus

406   unable to correlate species decomposition rates to species leaf litter qualities and/or species site

407   condition specialization/association. Examining such correlations may reveal the subtler effects

408   of leaf litter chemistry on decomposition rates and may allow the investigation of the of HFA at

409   micro spatial resolutions (e.g., in the immediate vicinity of parent trees).

410

411 **TABLES**
412
413 **Table 1.** Coefficient estimates with their associated confidence intervals and model selection metrics of all models of remaining leaf
414 litter dry mass. The interaction terms containing *Plot* and *Origin* estimate the differences in the response when the plot type or litter
415 origin are swamp plots or swamp tree species, instead of dry plots or non-swamp tree species, respectively. *Prop. remain* = the logarithm
416 of the proportion of remaining mass after accounting for handling loss; R^2m = marginal R^2, the explanatory power of only the fixed
417 effects terms of the models; R^2c = conditional R^2, the explanatory power of both the fixed- and random- effects terms of the models.
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419

Model rank	Prop. remain (intercept)	Initial mass	Duration	Duration × Plot	Duration × Origin	Duration × Plot × Origin	df	ΔAICc	Weight	R^2m	R^2c
1	0.603 (±1.066)	0.549 (±0.586)	−0.0066 (±0.0005)	0.0048 (±0.0006)	–	–	8	0.000	0.427	0.729	0.729
2	0.679 (±1.068)	0.508 (±0.587)	−0.0068 (±0.0006)	0.0048 (±0.0006)	0.0004 (±0.0006)	–	9	0.456	0.340	0.730	0.730
3	0.688 (±1.062)	0.503 (±0.583)	−0.0070 (±0.0006)	0.0052 (±0.0008)	0.0007 (±0.0008)	−0.0007 (±0.0012)	10	1.217	0.233	0.731	0.731
4	0.794 (±1.138)	0.445 (±0.624)	−0.0043 (±0.0005)	–	–	–	7	145.460	<0.001	0.636	0.636
5	0.885 (±1.142)	0.396 (±0.626)	−0.0045 (±0.0006)	–	0.0005 (±0.0007)	–	8	145.628	<0.001	0.637	0.637
6	0.766 (±1.337)	0.370 (±0.734)	–	–	–	–	6	380.779	<0.001	0.415	0.415

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FIGURE LEGENDS

Figure 1 (a) Locations within the Nee Soon freshwater swamp forest of the ten plots used in this study, and (inset) location of the Nee Soon freshwater swamp forest within the island of Singapore; (b) two-dimensional nonmetric multidimensional scaling (NMDS) plots of canopy tree (summed basal area per plot of all trees larger than 5 cm diameter at breast height) communities in these ten plots, showing the strong divergence in tree communities on non-swamp (green triangles) and swamp (blue circles) plots (points which are closer together have more similar communities); points represent plots, while text represent species centroids, which are scaled according to total basal area (rare species are not displayed), stress = 0.092, the full list of unabbreviated species names are provided in Table S1 of the online supplementary information. (c) Example of a leaf litter trap (indicated by arrow) within a swamp plot.

Figure 2 (a) Ranking of variables by the sum of their variable weights. Variables with low summed weights were only found in models that were poor fits to the data. (b) Best model predictions of litter dry mass as a function of decomposition duration (number of days litter bags were placed in the field). Lines represent model predictions, while each point represents the observation of a single litter bag. (c) Comparison of differences in medians (points) of decomposed litter proportion between litter of different origins (remaining litter proportion of non-swamp tree species minus that of swamp tree species), in non-swamp and swamp plot types over time. A positive difference means that litter of non-swamp origin decomposed faster than that of swamp origin. Vertical lines about the points represent bootstrapped 95% confidence intervals from different batches of litter bags deployed. In (b) and (c), filled circles and black lines represent data from non-swamp plots, while open circles and grey lines represent data from swamp plots.

Figure 3 Comparison of C:N ratio between leaf litter of the best represented morphospecies collected from leaf litter traps in swamp and non-swamp plot types. Bold lines represent group medians; boxes represent interquartile ranges; whiskers represent maxima/minima; and points represent outliers.
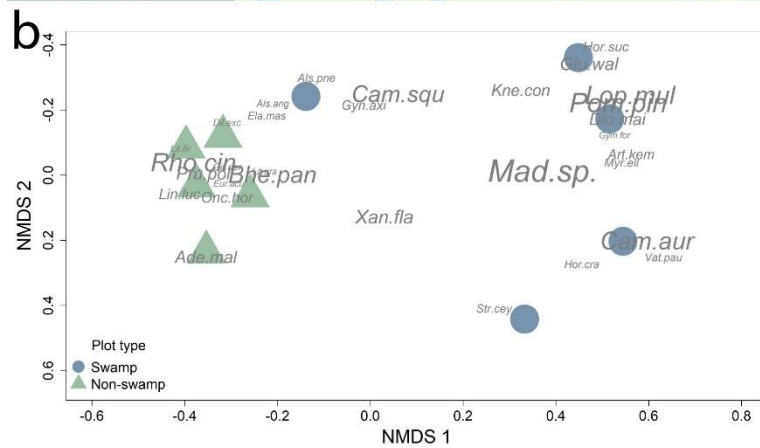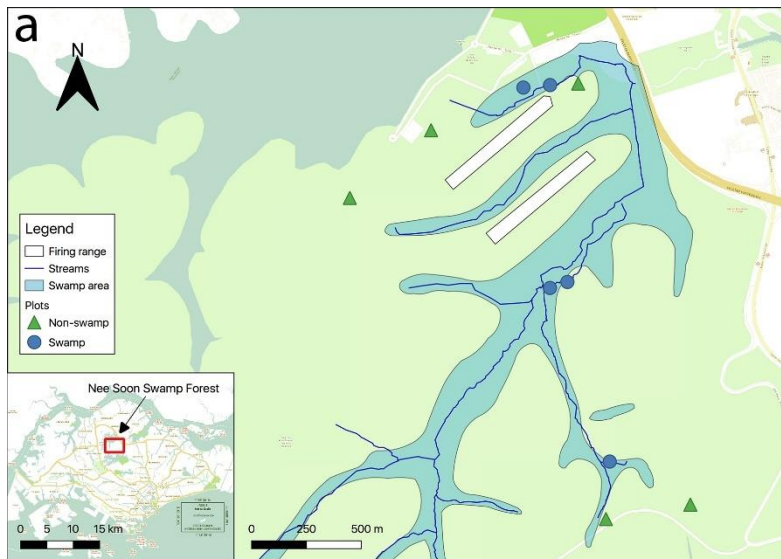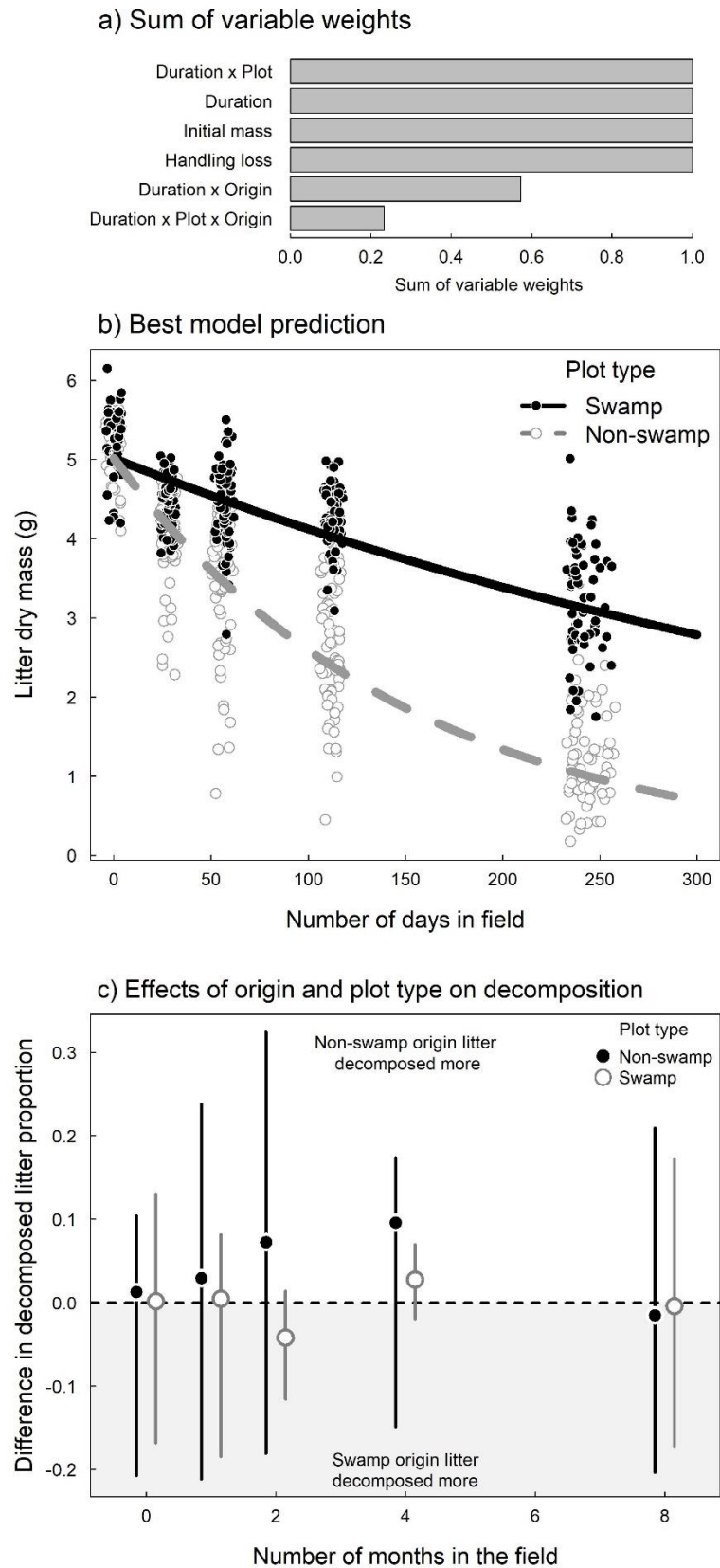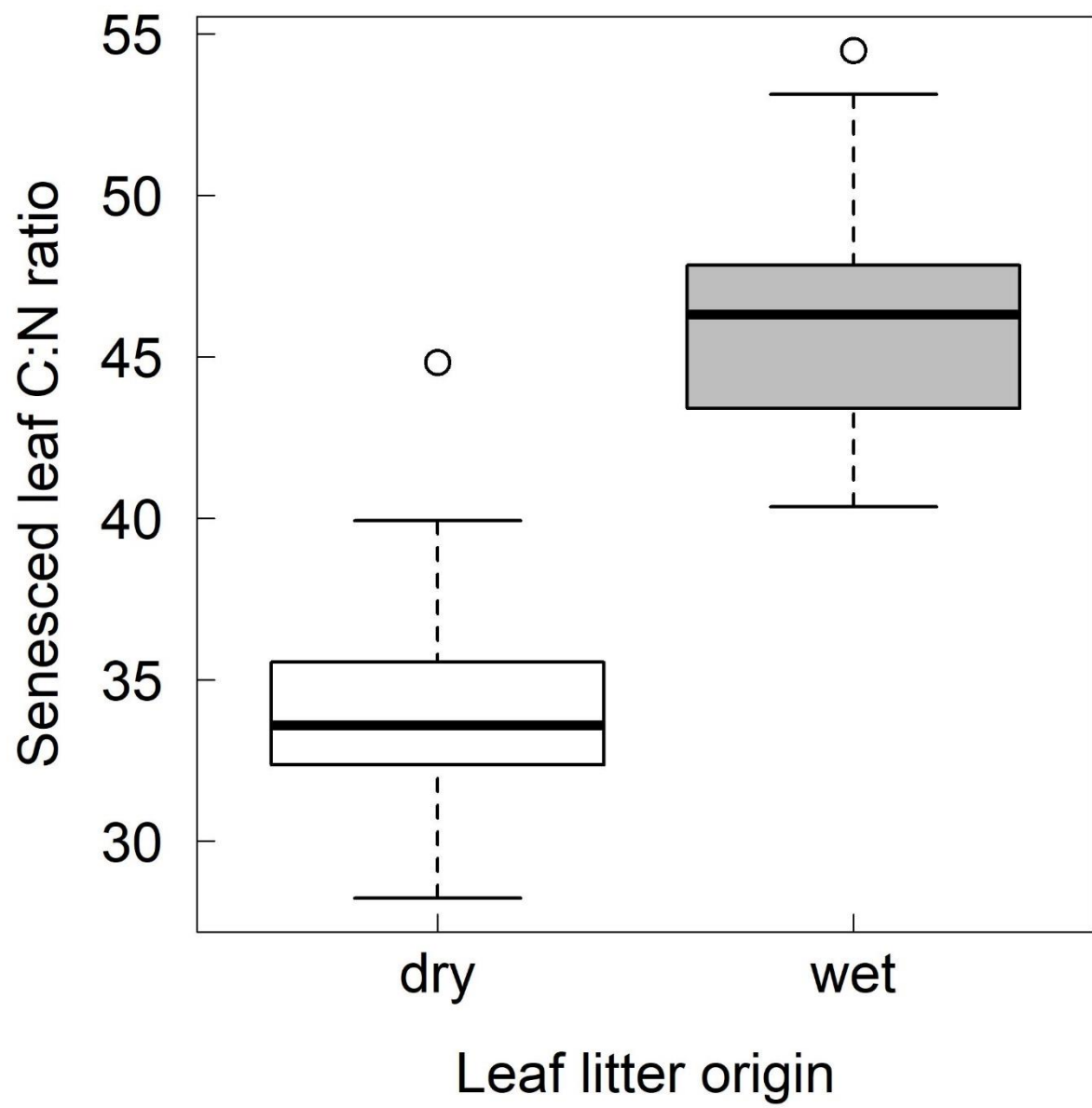
456
457 **Figure 1**

a) Sum of variable weights

b) Best model prediction

c) Effects of origin and plot type on decomposition

460
461 **Figure 3**
462

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AUTHOR CONTRIBUTION STATEMENT

JJL, KYC, SJR and KSHP designed the study; JJL, PJC, YYT, RC, NER, LWAT, QYH and WNL collected the data; WNL and JJL analysed the data; WNL wrote the first manuscript draft; all authors contributed to subsequent revisions, and gave final approval of the manuscript for submission.

DATA AVAILABILITY

The data that support the findings of this study will be made openly available on the Dryad

digital repository upon publication at http://doi.org/, reference number.

COMPETING INTERESTS

We declare we have no competing interests.

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