

Land use and multidimensional diversity jointly shape carbon stocks in an Indonesian seasonally dry ecosystem

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Running title: Multidimensional diversity shapes carbon stocks

27 **Abstract**

28 Dry ecosystems are critical to the global carbon cycle. Seasonally dry tropical ecosystems
29 as a whole are botanically megadiverse yet we have little understanding of how diversity
30 impacts aboveground carbon, this being particularly noticeable for insular Asia. Across
31 133 vegetation plots on the seasonally dry tropical island of Flores we used spatially
32 explicit models to determine how land use impacts aboveground carbon stocks and
33 whether this is dependent upon multidimensional diversity. Carbon is greatest in primary
34 forests and least in agricultural landscapes. However, we find that land use interacts with
35 phylogenetic and species diversity to shape carbon stocks. Across almost all models,
36 quadratic effects of diversity were better predictors of carbon, indicating that whilst the
37 initial build-up of diversity increases carbon, greater diversity causes carbon decline.
38 Results suggest future conservation plans will need to balance carbon storage with
39 multidimensional diversity which may offer distinct benefits for ecosystem resilience and
40 services.

41 **Keywords**

42 Biomass, Dry forest, Ecosystem function, Flores, Wallacea

43 **Introduction**

44 The global carbon cycle that underpins all life on earth is dependent upon the forested
45 ecosystems of the tropics (Lewis *et al.* 2015). Carbon maintained in woody biomass
46 restricts the amount of atmospheric carbon, limiting the rise in global temperatures
47 (Guillaume *et al.* 2018; Pan *et al.* 2011). Carbon stocks are dependent upon community

diversity via multiple indirect effects (Grace *et al.* 2010; Liang *et al.* 2016; Tilman *et al.* 2014). These include impacts upon how efficiently resources are taken up and converted to biomass (Hodapp *et al.* 2019). Species-specific pathogen and herbivore impacts are also limited by greater diversity (Parker *et al.* 2015). Whilst there has been evidence of diversity-carbon storage links across wet tropical forests it is less clear whether this is reflected in the seasonally dry tropics (Dexter *et al.* 2018; Godlee *et al.* 2021; Miles *et al.* 2006; Murphy and Lugo 1986). Drylands are a critical and growing component of the global carbon stock (Ahlström *et al.* 2015). Subsequently, they are key to carbon cycling (Fawcett *et al.* 2022). Despite this, dryland climates often make for productive agricultural lands leading to their conversion (Lewin *et al.* 2024). Drylands are also expected to be at risk from global temperature rise, this is coupled with lower formal conservation designation than non-drylands (Huang *et al.* 2017). It is therefore crucial to understand the importance of dryland diversity for ecosystem function, so biodiversity conservation can be prioritised (Hanan *et al.* 2021).

Diversity controls carbon stocks in grass-dominated dry ecosystems in Africa (Godlee *et al.* 2021; Pelletier *et al.* 2017). Caatinga dry forest biomass likewise show diversity dependent biomass (Gomes Souza *et al.* 2019). However, more widely across neotropical dry forests, diversity shows little sign of a relationship with carbon stocks (Mora *et al.* 2018). Studies on the tropical islands of Asia are conspicuous in their absence (Becknell *et al.* 2012). Asian dry forests are found from India to the Lesser Sunda archipelago of Indonesia (Ratnam *et al.* 2016). Ecophysiological constraints of drought result in plant community species composition quite distinct from the rest of wet tropical Asia (Kalkman

1955; Baltzer *et al.* 2008; Rustiami *et al.* 2020; van Steenis 1979). The Lesser Sunda archipelago is a chain of small islands, the largest Timor being only 28,418 km². The subsequent minimal interior of these small islands leads to a greater proportion of the natural vegetation being exposed to the predominantly coastal human communities. The coastal human communities exploit the vegetation as a source of timber, food products, and indirectly water via the protection of watersheds (particularly important during the months of low precipitation) (Beller *et al.* 1990; Pattanayak and Wendland 2007). It is unclear how land use impacts carbon storage in the Indonesian seasonal forest ecosystem and how sensitive stocks are to changing diversity (Jew *et al.* 2016; McNicol *et al.* 2018; Ruiz-Jaen and Potvin 2011; Silva Pedro *et al.* 2015).

Consensus has yet to be reached on the form of the relationship between diversity and carbon stocks. Linear positive relationships are often assumed where greater diversity results from efficient niche partitioning and resource use that benefits biomass production (Poorter *et al.* 2015; Ruiz-Benito *et al.* 2014). Likewise, greater diversity can increase the chance that high-carbon individuals will be present (Carol Adair *et al.* 2018; Cavanaugh *et al.* 2014; Loreau and Hector 2001). Alternatively, at higher diversity, carbon storage may plateau or even decrease, caused by more competitive, low-carbon individuals (Aponte *et al.* 2020; Conti and Díaz 2013). Therefore, quadratic effects of diversity upon carbon storage may occur where an initial increase is followed by saturation and/or decline. Despite the often observed parabolic relationship, linearity between biodiversity and carbon is often predicted. Here we test whether that is the case on the Lesser Sunda island of Flores.

Communities contain a combination of species, their evolutionary history, and their traits (e.g. Chao *et al.* 2014a). These features combine as potential multidimensional controls upon carbon storage (Tilman *et al.* 2014). Calculated via species identification, measurements of evolutionary tree topology, and trait (e.g. leaf area, height etc.) ordination space, they offer complementary information that impact niche packing, resource use and abundance (Conti and Díaz 2013; Mensah *et al.* 2016; Ouyang *et al.* 2016). How fluctuation of these three measures of diversity mediates carbon storage across seasonally dry land use types requires study to determine the importance of species for conservation plans primarily focused upon ecosystem function.

Whilst niche packing is invoked as a driver of productivity and biomass stocks via ties to efficiency of resource use in the local environment (Tilman *et al.* 2014). Species niche is a function of interactions across guilds, including non-woody species that store minimal carbon. Here we use all plant species to calculate diversity metrics. This ensures we account for more competing and facilitating species, than using tree species alone. These metrics include trait diversity where we gather reproductive and dispersal linked trait data, alongside more commonly studied traits such as plant and leaf size, to better encompass niche axes and provide a metric better linked to the niche space occupied by the community (E-Vojtkó *et al.* 2022; McFadden *et al.* 2022).

Land use impacts diversity by altering the conditions for species reliant upon minimal human impact (Alroy 2017). With greater human resource use, e.g. logging, species are removed and species that favour disturbance begin to dominate (Carreño-Rocabado *et al.* 2012; Sheil and Burslem 2003). As human resource use in a landscape increase toward

agriculture planted species become present (Barlow *et al.* 2007). These changes have knock-on effects upon diversity but also aboveground biomass (Avila *et al.* 2018). How variation in diversity and land use changes across Indonesian dry ecosystems is little known as are their joint effects upon aboveground biomass.

Whilst studies of Indonesia's seasonally dry plant diversity are growing (Laumonier and Nasi 2018; Simbolon 1999; Sumadijaya *et al.* 2024; Sutomo *et al.* 2020, 2021; Trethowan 2021; Wiriadinata *et al.* 2013), assessments of its relationship with carbon storage are few. Here, we use data from a landscape with a gradient from high to low forest management in western Flores to test two hypotheses (1) aboveground carbon stocks are determined by the interaction of land use and species, phylogenetic and trait diversity and (2) that a linear relationship best fits the interaction effects of diversity.

Methods

Site description, plot establishment and aboveground biomass

One hundred and thirty-three 20 m x 50 m plots were established in the seasonally dry landscape of Mbeliling, West Manggarai district (119.78 E to 120.30 E, -8.53 S to -8.87 S) on the island of Flores (Fig. 1a, Tab. S1). West Manggarai mean air temperatures range from 26.6 to 28.2 °C. Relative humidity varies between 71 and 88 % and annual precipitation 1700 mm to 2400 mm. We sampled locations with increasing intensities of land use in three broad categories of primary, secondary, or agricultural sites. We removed 13 mangrove and savanna plots. The 35 primary sites were relatively untouched by humans. The 51 secondary sites were forests that had been logged or damaged by trails (38) or

forests that had been completely destroyed and begun to regrow - often appearing shrubby (13). The 34 agricultural sites were teak plantations (7) or farmlands planted with non-rice crops and timber species (27; Fig. 1a).

All trees > 35 cm diameter at breast height (1.3 m, dbh) were recorded from each 20 m x 50 m plot. Nested within each of these plots, all trees > 20 cm dbh were recorded in a 20 m x 20 m subplot. All trees > 10 cm dbh were recorded in a 10 m x 10 m subplot. All individuals > 2 cm dbh and height > 1.5 m were recorded in a 5 m x 5 m subplot and all individuals irrespective of diameter were recorded in a 2 m x 2 m subplot. This method (Hairiah *et al.* 2001) allowed us to sample across all guilds that contribute to seasonal plant communities (Devecchi *et al.* 2020). Most individuals (93 %) were assigned to a species or named morphospecies. The few unidentified individuals were removed from all analyses resulting in 126 named species and morphospecies. We calculated aboveground biomass *AGB*, our measure of carbon storage, for all trees > 10 cm dbh using hypsometer-measured height *H*, diameter at breast height *D* and wood density *WD* acquired from previously published datasets (Chave *et al.* 2014) using the biomass package (Réjou-Méchain *et al.* 2017). For this we discarded bamboo, palm and liana species as their carbon stocks are poorly predicted by allometric equations (Chave *et al.* 2014). *AGB* calculation used the following equation from Chave *et al.* (2014):

$$AGB = 0.0673 + (WD * H * D^2)^{0.976}$$

154 To calculate AGB for the entire 20 m x 50 m plots we multiplied the trees sampled in
 155 subplots: those > 10 cm dbh and < 20 cm dbh in 10 m x 10 m subplots by 10 and those > 20
 156 cm dbh and < 35 cm dbh in 20 m x 20 m subplots by 2.5.

157 **Environmental covariate**

158 To ensure our results were not a function of environmental variation across the landscape,
 159 we accounted for it across models (Corona-Núñez *et al.* 2018). For each plot we
 160 downloaded fifteen ‘bioclim’ variables from Worldclim (Fick and Hijmans 2017). Eight
 161 climatic variables were log-transformed (mean annual temperature, maximum
 162 temperature of the warmest month, minimum temperature of the coldest month, mean
 163 temperature of the wettest quarter, mean temperature of the driest quarter, mean
 164 temperature of the warmest quarter, mean temperature of the coldest quarter,
 165 precipitation seasonality) and seven were not transformed (annual precipitation,
 166 precipitation of the wettest month, precipitation of the driest month, precipitation of the
 167 wettest quarter, precipitation of the driest quarter, precipitation of the warmest quarter,
 168 precipitation of the coldest quarter). Non log-transformed elevation data from the Shuttle
 169 Radar Topography Mission was used (Farr *et al.* 2007). Bulk density of fine earth fraction,
 170 volumetric fraction of coarse fragments, pH, sand in fine earth and soil organic carbon
 171 from SoilGrids were included (Hengl *et al.* 2017). There was a single principal component
 172 axis of environmental variation between sites that explained 93 % of the variation in the
 173 scaled (z-scores) environmental data. This was retained as an environmental covariate
 174 across all models.

175 **Trait data**

176 We gathered traits for 126 species from taxonomic publications, compiling data on plant,
 177 leaf and fruit size, plant habit and flower size and colour. We had five dichotomous plant
 178 habit variables: tree, shrub, climbing, herb and epiphyte. Leaf shape were designated as
 179 either obovate, oblanceolate, palmately lobed, ovate, elliptic, lanceolate, linear, orbicular
 180 or oblong (Schrader *et al.* 2021). Other leaf shape designations were placed within this
 181 framework e.g. sublanceolate became lanceolate and subobovate became obovate. We
 182 used the largest recorded measurements for plant size (herb, shrub, tree height or liana
 183 length) and for the two leaf size categories, length and width (Trethowan *et al.* 2022). Leaf
 184 area was calculated as leaf length multiplied by leaf width multiplied by a leaf shape
 185 correction factor (Schrader *et al.* 2021). For fruit size, we used the largest recorded
 186 measurement of either length or width (Trethowan *et al.* 2023). Flower size was the largest
 187 recorded measurement of either calyx, corolla or stamen length (Trethowan *et al.* 2024b).
 188 Flower colour was split into seven dichotomous variables: red, yellow, white, purple, pink,
 189 orange and brown (Trethowan *et al.* 2024b). This data was not collected in the field and
 190 intraspecific variation could lead to trait differences on the ground in Flores. All continuous
 191 data were log-transformed and scaled as z-scores prior to trait imputation, co-occurrence
 192 modelling, and trait diversity calculation.

193 To fill continuous and categorical trait data gaps, we ran random forests incorporating the
 194 ten first selected phylogenetic eigenvectors to aid imputation accuracy (Carmona *et al.*
 195 2024; Penone *et al.* 2014; Stekhoven and Bühlmann 2012). Missing data were far below the
 196 70 % threshold where diversity indices are expected to be affected post gap-filling (Stewart

et al. 2023). Imputation models were iterated 15 times and species mean values calculated for each continuous trait and the most frequently predicted value for categorical traits was selected.

The phylogeny used for imputation was built for all species in the dataset and assumed a Brownian motion model of evolution (Li *et al.* 2020a). To construct the phylogeny, dated phylogenetic data were acquired from published phylogenies (Jin and Qian 2019). When only genera were present in the backbone phylogeny, species were added as a polytomy at the root node (i.e., most recent common ancestor) of the genus. Genera not present in the backbone phylogeny were bound to the halfway point between the family root node and basal node. When the family branch length was longer than two thirds from the family root node to the tip, the genus was bound to the upper third of the whole family branch length (Jin and Qian 2019; Qian and Jin 2016). This followed methods implemented previously using different software i.e., Phylomatic and BLADJ (Webb *et al.* 2008).

Multidimensional diversity calculation

Species, phylogenetic and trait diversity metrics followed the Hill number framework (Chao *et al.* 2014a). Hill numbers obey the replication principle in that when two assemblages have zero species in common and identical relative abundance distributions, when summed they have twice as great diversity. This is not the case for classic abundance weighted diversity measures e.g. Shannon entropy and Gini-Simpson (Chao *et al.* 2014a; Jost *et al.* 2010).

For all diversity metric calculations we used species abundances. We extrapolated the Hill species diversity metric to give 98.5 % species coverage for plots without abundance weighting ($q=0$) following published recommendations (Chao *et al.* 2014b; Hsieh *et al.* 2016) and repeated this method for phylogenetic and trait diversity. Phylogenetic extrapolations were of total branch length from the root node, and trait diversity from the summed number of functional entities which were those entities that exceeded the threshold of the mean distance between any two individuals randomly selected from the pooled assemblage (Chao *et al.* 2014a, 2015). The trait distances were Gower distances with each flower colour and habit down-weighted so that the total weights for flower colours and habits was equal to the continuous trait variables of plant, flower and fruit size and leaf area. Leaf area was retained rather than leaf shape, length, and width as it is more tightly linked to plant function (Li *et al.* 2020b). The community phylogeny used for total branch length calculation was identical to that used for trait imputation above.

Statistics

To avoid spatial autocorrelation, we assessed our hypotheses with a series of spatial simultaneous autoregressive lag models of AGB (Bivand *et al.* 2013; Bivand and Piras 2015). Here, predictions are also dependent upon the value of neighbouring plots, ensuring results account for plots that are closer together more likely having similar AGB and limiting potential inflation of effect score estimates (Darmofal 2015). Neighbours were determined by a spatial covariance matrix resulting from the scaled exponential distances between plots (French 2018). The general statistical model structure was as follows:

$$AGB = \alpha\gamma + \delta$$

The land use parameter γ was a dichotomous variable for either agriculture, secondary or primary forest (hypothesis 1). Models were iterated for each land-use type, for instance the γ parameter for agriculture models is a categorical variable of either ‘agriculture’ or ‘non-agriculture’. We iterated in this fashion as we were not confident of the order in the magnitude of effect between agriculture, secondary and primary forest upon AGB. Diversity α was either species, phylogenetic or trait diversity (hypothesis 2). This gave us nine parameter combinations. We also ran models with quadratic diversity effects and calculated Akaike Information Criterion (AIC) to compare model error between quadratic or linear effects (hypothesis 2). A total of 18 models were built to cover all parameter combinations and quadratic or linear effects of diversity α . The environmental covariate δ was identical across all models.

Results

Land use impacts upon AGB

Models showed that primary forest plots had greater AGB (mean effect upon AGB (effect score) = 0.88, mean standard error (se) = 0.29) than non-primary plots (Fig. 1b). Agricultural plots had lower AGB (effect score = -0.34, se = 0.24, Fig. 1b), as did secondary forests (effect score = -0.42, se = 0.35, Fig. 1b).

Joint land use and diversity effects upon AGB

Diversity measures' direct effects upon AGB were inconsistent, in terms of both direction and size, in addition to frequently having large standard errors (Supplementary Material Tab. 1). The interaction between land use and diversity, however, often had consistent effect directions across models irrespective of the form of the effects of diversity upon AGB (Fig. 1c). For instance, primary forest interaction with trait diversity had consistently negative effects upon AGB with both linear (effect score = -0.02) and quadratic diversity effects (effect score = -0.58, Fig. 1c).

All models except for that parameterised by phylogenetic diversity and secondary forest status (and their interaction) had reduced lower prediction error with quadratic diversity effects (Fig. 1d). The greatest improvement was in the model parameterised by trait diversity and primary forest status, and their interaction (Fig. 1d).

Amongst the models with consistent effects of the interaction between land use and diversity (Fig. 1c, where effect score bar do not approach zero), all models had reduced model error with quadratic effects (Fig. 1c). The models in question were two parameterised by phylogenetic diversity and its interaction with primary forest and agriculture, two with species diversity and its interaction with primary and secondary forest parameters, but no models parameterised by trait diversity (displayed in Fig. 1e). Quadratic diversity effects were overall negative (Tab. S2) indicative of the concave relationship, e.g. peak followed by decline, with AGB.

Discussion

277 We have shown that land use impacts above-ground carbon stocks in the dry tropical
278 forests of Indonesia (hypothesis 1) but that whilst this is mediated by diversity (hypothesis
279 2) it is best predicted by the quadratic effects of diversity. Which suggests, that whilst
280 accounting for the effects of land use, when diversity increases carbon storage increases
281 to a point but with ever increasing diversity carbon stocks will plateau or even decline in
282 the seasonally dry forests of Indonesia.

283 In the west Flores landscape, we show that phylogenetic and species diversity are more
284 influential for carbon stocks than trait diversity. For phylogenetic diversity there are
285 contrasting effects for agricultural and primary forests. Agricultural landscapes carbon
286 stocks benefit from more lineages but primary landscapes do not. Primary landscapes also
287 have a negative relationship with species diversity. Interestingly, species diversity did have
288 a positive interaction with secondary forests. Across guild species diversity is also slightly
289 greater in secondary forests than primary. This suggests that more species and lineages
290 doesn't guarantee a more carbon-dense community in primary landscapes but can for
291 those with greater human influence where diversity may likewise be greatest (Flynn *et al.*
292 2011; Mensah *et al.* 2020; Tolmos *et al.* 2024). We found little interaction between trait
293 diversity and land use in shaping carbon stocks. Our focus upon across guild diversity may
294 be linked to this; where previous evidence of the importance of trait diversity was linked to
295 tree species (Conti and Díaz 2013), we found that land use effects upon carbon were
296 independent of trait diversity for a larger cross-section of the plant community.

297 Our results show that the impacts of secondary forest effects upon carbon stocks
298 interacts positively with species diversity and to a lesser extent phylogenetic diversity.

299 These secondary forests have been shaped by disturbance and succession, both of which
300 may exacerbate diversity impacts upon carbon storage (Lasky *et al.* 2014). During
301 succession, fast growing ruderal species may accumulate carbon and for these taxa
302 greater phylogenetic and species diversity may result from their survival despite the risk of
303 or prior to being outcompeted as succession proceeds (Lasky *et al.* 2014).

304 We present a study that incorporates fruit and flower traits into trait diversity metrics.
305 These traits are representative of niche axes linked to dispersal and reproduction. These
306 traits can influence the overall energy budget of plants with potential consequences for
307 biomass (Salguero-Gómez 2017). Plus, they shape the ability to recruit new individuals
308 locally or the likelihood of replenishment from a wider metapopulation which may
309 determine survival and thus carbon stock retention of individual species (Fricke *et al.*
310 2025). There are however, other traits often used as single parameters of productivity and
311 biomass such as specific leaf area, tree maximum height and wood density (Finegan *et al.*
312 2015; Ruiz-Jaen and Potvin 2011). The quadratic effects of trait diversity that we found may
313 not hold if those traits are examined, however our results encompass trait diversity across
314 guilds, providing a different and complementary insight from studies focused solely upon
315 trees.

316 We show that diversity and carbon storage do not consistently covary across land use
317 types in west Flores. This adds to the evidence base that conservation plans across
318 landscapes of varying human impact will require separate priorities for both biodiversity
319 and carbon (Ferreira *et al.* 2018; Thomas *et al.* 2013; Zhu *et al.* 2021). It has been suggested
320 that conservation of secondary forests will be key to these strategies, and our results

suggest that is the case in Flores. Although if, as expected, secondary forests are more accessible and in regions of greater human population density then their land value will be such that it may be more cost-effective to conserve primary forests (Malhi *et al.* 2022; Phelps *et al.* 2012; Van de Perre *et al.* 2018). Remotely sensed carbon stocks can easily be incorporated but plant diversity layers are still required to inform evidence-based spatial conservation plans. Our results suggest that high multidimensional diversity landscapes may not be carbon priorities, yet these may be diversity source regions and may be more stable when exposed to novel climates (Gallagher *et al.* 2013).

Our findings replicate studies across other seasonally dry landscapes showing how carbon storage shifts with land use and biodiversity (Becknell *et al.* 2012; Godlee *et al.* 2021).

Other ecosystem functions and services such as pollination and the availability of useful plants are largely unknown at fine scales across the islands from Sumatra to New Guinea (Cámara-Leret *et al.* 2019; Pironon *et al.* 2024; van der Plas *et al.* 2018). As such, we do not yet have clear baseline knowledge of the interactions between pollinators, plant diversity and carbon, which will be key to understanding climate change impacts upon these megadiverse islands and the knock-on effect for urban and rural livelihoods (Dubois *et al.* 2014; Feng *et al.* 2013; Struebig *et al.* 2015; Wolff *et al.* 2021). Our work complements ongoing efforts to assess American, African and continental Asian dry forests (Chaturvedi *et al.* 2011; Godlee *et al.* 2021; Portillo-Quintero *et al.* 2015; Yang *et al.* 2023). There are further dry tropical ecosystems in the Lesser Sunda Islands and Papua that still require field-based diversity and carbon data (Laumonier and Nasi 2018; Trethowan *et al.* 2024a). Field-based carbon stock data collation is likewise warranted from all the tropical islands

343 of Malesia and will help address a major gap in global analysis (Anitha *et al.* 2015; Qie *et al.*
344 2017; Slik *et al.* 2010; Sullivan *et al.* 2017).

345 We offer evidence that land use and diversity together impact dry ecosystem aboveground
346 carbon stocks. However, diversity effects follow a quadratic form potentially indicative of
347 declining facilitation toward greater competition with negative consequences for carbon.
348 Although models of carbon stocks through time would be required to determine this in
349 more detail. Overall, multidimensional diversity has complex relationships with carbon
350 across land use types and may require distinct conservation strategies across insular dry
351 forests of Asia.

352 Authors' contributions: Wahyu C. Adinugroho, Liam A. Trethowan, Francis Q. Brearley and
353 Rinaldi Imanuddin designed the study, implemented it and contributed to the development
354 of the manuscript. Wahyu C. Adinugroho and Rinaldi Imanuddin led study site selection,
355 field sampling and data collection. Wahyu C. Adinugroho, Rinaldi Imanuddin, Asep Ayat
356 and Lalu Abdi Wirastami participated in field data collection. Renata Borosova, Marie
357 Briggs, Osanna Chu, Sally Dawson, Grace Flanagan, Laura Jennings, Cecilia Lee-Grant,
358 Alison Moore, Shawn O'Donnell, Carmen Puglisi and Mariana H. Santana gathered trait
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361 Data availability: The datasets used and/or analysed during the current study are available
362 from the corresponding author on reasonable request. Rmd file to run analyses and build
363 manuscript is available at https://figshare.com/authors/Liam_Trethowan/8268603.

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372

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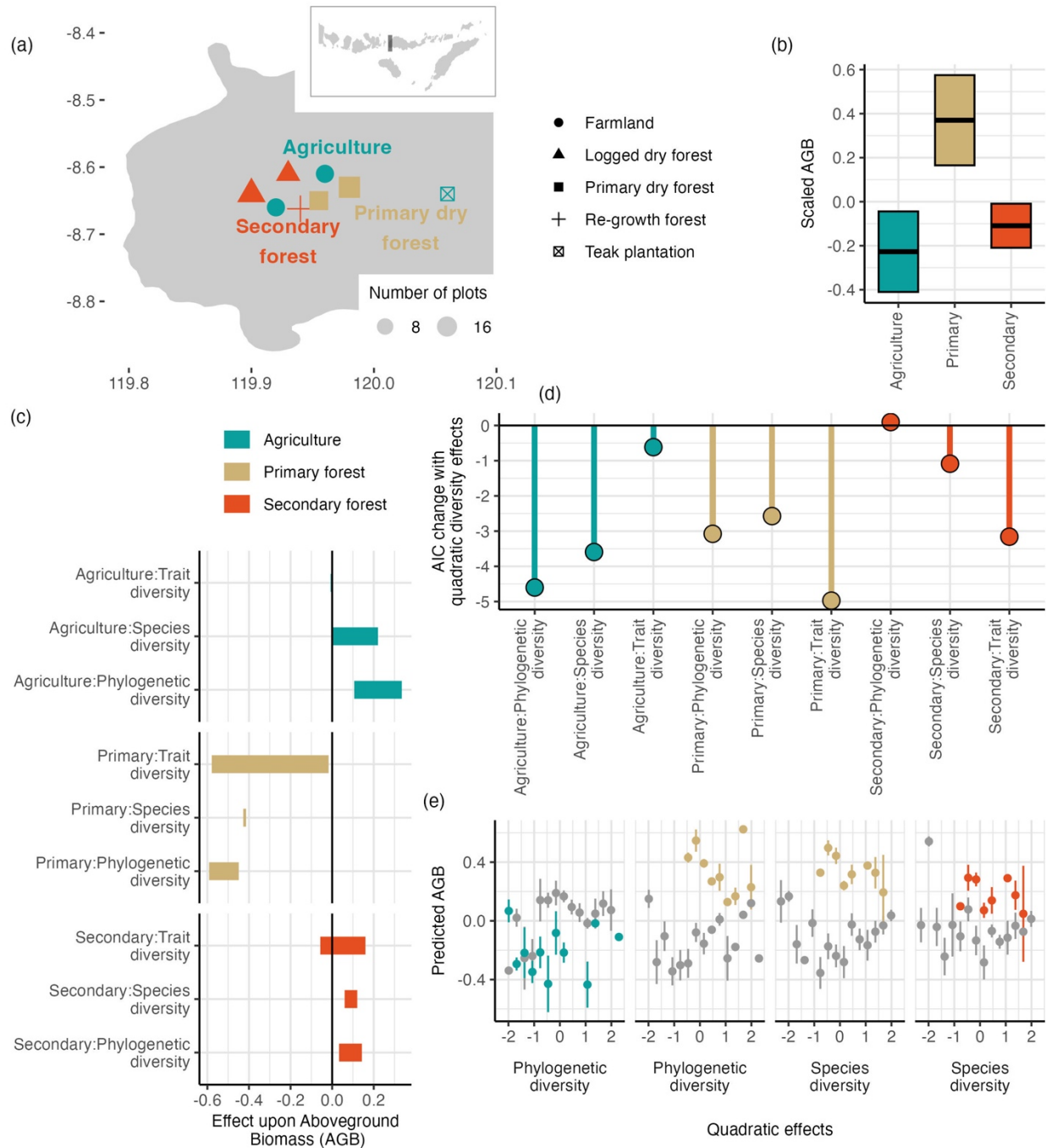


Figure 1: (a) Map of vegetation sampling sites in west Flores, Indonesia. **(b)** Mean and standard error aboveground biomass (AGB) across land use types. **(c)** Diversity and diversity land use interaction effect size range across models of AGB. Linear and quadratic diversity effects presented. **(d)** Differences in model error, measured by the Akaike

846 Information Criterion (AIC), between models parameterised by quadratic or linear effects
847 of diversity. **(e)** Predicted AGB from the four models with consistent land use diversity
848 interactions and lowest error rates (AIC). Colours represent plots of land use type included
849 as the parameter in the model, grey points represent plots that are not within that type as
850 specified in that model. For example, the left-hand panel shows secondary forests in red
851 and grey represent primary and agricultural plots.

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