

Incorporating habitat suitability into community projections: Ant responses to climate change in the Australian Wet Tropics

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Abstract

Aim: Studies of climate change impacts on animal distributions typically consider only the direct impacts of a changing climate, under the assumption that future areas of suitable climate will otherwise remain ecologically suitable. Here we assess both the direct and indirect impacts of climate change on rain forest ant communities, where substantial shifts are projected to occur for both climate and habitat types.

Location: Australian Wet Tropics (AWT).

Methods: Generalized Dissimilarity Modelling was used to model turnover in the composition of ~300 rain forest ant species sampled at 150 sites across six mountains spanning five degrees of latitude. Ants were sampled within the leaf litter, on the litter surface and on tree trunks. By modelling the rate of turnover among sites, we determined the current effective area of similar ecological environments (SEE) for ant communities and consequently the expected change in species persistence when habitat shifts under two climate projections for the years 2035, 2055 and 2085. We compared results when SEE considered only the direct effects of a changing climate, with those when changes in habitat were also included.

Results: The rain forest ant communities modelled will lose a substantial proportion of SEE under both climate change scenarios. Under combined direct (changes in climate) and indirect (changes in rain forest habitat) impacts of climate change, >90% of the communities in the region were predicted to lose up to half their similar habitats compared with 50%–60% when only considering direct climate change impacts. The highest risk of reduction in area of SEE is projected in drier inland areas of the AWT, where profound compositional turnover is linked to dramatic changes in rain forest vegetation, including extensive conversion into savanna.

Main conclusions: Our findings emphasize the importance of incorporating habitat suitability into future projections of species turnover under a changing climate, particularly for habitats where vegetation structure is projected to undergo profound change.

KEYWORDS

climate change, composition turnover, ecological environments, GDMs, habitat condition, rain forest

1 | INTRODUCTION

Anthropogenic climate change and associated extreme weather events are predicted to significantly alter species distributions and subsequently the composition of biological communities (Arribas, Abellán, Velasco, Millán, & Sánchez-Fernández, 2017; Huey et al., 2012; Jenkins et al., 2011; Thomas, 2010). Rising temperatures might cause metabolic, behavioural or evolutionary change in species, or drive dispersal to climatically suitable areas (Parmesan, 2006; Reuman, Holt, & Yvon-Durocher, 2014; Urban, Tewksbury, & Sheldon, 2012). Community-level responses are more complicated, as changing temperature is likely to have differential effects among species (Elmendorf et al., 2012). Species interactions also may change disrupting mutualisms, trophic interactions, competitive hierarchies and ultimately species occurrence (Blois, Zarnetske, Fitzpatrick, & Finnegan, 2013; Sentis, Hemptinne, & Brodeur, 2014; Sorte & White, 2013). Therefore, forecasting changes in the distribution and composition of biological communities under future climates can be extremely challenging.

The potential decoupling of species associations due to differential climate change sensitivity can have particularly dramatic implications if vegetation and its associated fauna are differentially sensitive (Caddy-Retalic et al., 2018; Carvalho, Brito, Crespo, & Possingham, 2010; Garcia, Cabeza, Rahbek, & Araújo, 2014). Studies of climate change impacts on animal distributions typically consider only the direct impacts of a changing climate, under the assumption that future areas of suitable climate will otherwise remain ecologically suitable. However, this would not be the case if changes in climate indirectly reduce habitat suitability. This might occur as a direct response of vegetation to a changing climate, or indirectly through changes in, for example, fire regimes (Davis, Higuera, & Sala, 2018; Regos, Claverio, & D'amen, Guisan & Brotons, 2018). Changes in vegetation structure can have a greater effect on microclimate than changes in macroclimate (Williams, Bolitho, & Fox, 2003).

Vegetation change would be particularly dramatic for fauna if it rendered the habitat largely unsuitable. This is especially relevant in high-rainfall regions of the tropics where savanna and forest co-occur and readily transition from one to the other with changes in climate and fire regimes (Dantas, Hirota, Oliveira, & Pausas, 2016; Langan, Higgins, & Scheiter, 2017; Murphy & Bowman, 2012). Savanna and forest support highly disjunct faunas (Murphy, Andersen, & Parr, 2016), such that transition from one vegetation type to the other results in profound faunal change. For example, in northern Australia the ant faunas of co-occurring rain forest and savanna are remarkably distinct from each other (Andersen, Ingen, & Campos, 2008), with the rain forest fauna dominated by shade-tolerant, forest specialists, in contrast to the arid-adapted taxa that dominate savannas (Andersen et al., 2008; Reichel & Andersen, 1996). If forest switches

to savanna under future climates, then the habitat will be unsuitable for forest species even if the macroclimate is suitable for them. The critical role of the future distribution of habitats upon which species depend has been largely overlooked in studies regarding climate change impacts on biodiversity.

Changes in community composition can be modelled using stacked species distribution models (SDMs), but these have a poor record of predicting change even when environmental correlates of species occurrences are well known (D'Amen, Pradervand, & Guisan, 2015; Pellissier et al., 2013). One reason for this is that SDMs can predict if a species might occur in a general area that is climatically suitable, but they are limited when predicting if they will occur in any particular site, which may only have a fraction of the regional species pool, due to biotic interactions between species. Additionally, commonly used species-level modelling approaches (Elith & Leathwick, 2009) can vary in accuracy. For example, a developed modelling algorithm based on rank-ordered stacking of SDMs, compared to a binary stacking, can reduce variation of error in predicting community composition turnover along environmental gradients, but it still requires caution when predicting the species diversity (Del Toro, Ribbons, Hayward, & Andersen, 2018).

An alternative approach to predicting responses of biological communities to climate change is Generalized Dissimilarity Modelling (GDM), a nonlinear extension of matrix regression that models pairwise biological dissimilarity between sites as a nonlinear function of pairwise site difference in environmental and geographic variables (Brown, Cameron, Yoder, & Vences, 2014; Ferrier, Manion, Elith, & Richardson, 2007). Critically, by working directly with species assemblages, GDM can account for biotic interactions which are not typically included in SDMs. GDM extrapolates patterns of compositional turnover beyond sampled communities and is particularly well suited to communities with high levels of beta diversity. This analytical method can accommodate almost any measure of geographic or ecological separation as a predictor, including organism-specific representations of barriers to dispersal, or cost of movement/gene flow through unfavourable habitat (Fitzpatrick, Keller, & Vellend, 2015). GDM can also rapidly analyse datasets containing very large numbers of species, regardless of the number of records per species. Furthermore, by studying the emergent rates of spatial turnover along environmental gradients under current climatic conditions, GDM can be used to predict the temporal rate and spatial distribution of turnover under future climates (Blois, Williams, Fitzpatrick, Jackson, & Ferrier, 2013). Compared with SDMs, GDM can predict higher turnover and across a larger contiguous area (Fitzpatrick et al., 2011), where problems such as data limitations or indirect predictors such as habitat changes (Guisan & Thuiller, 2005) are likely to hinder the application of SDMs.

Generalized Dissimilarity Model commonly accommodates variation in rates of species turnover along environmental gradients (Fitzpatrick et al., 2013; Maestri, Shenbrot, & Krasnov, 2017; Penniford et al., 2017), but, unless programmed to do so, does not account for changes in habitat. However, GDM analyses can produce a variety of metrics to reveal and describe the relative biotic uniqueness of environments, and the proportion of those environments falling within different habitat classes (Jiménez-Alfaro et al., 2018; Johnston, Elmore, Mokany, Lisk, & Fitzpatrick, 2017). Therefore, it is important to simultaneously consider changes in both habitat and climate within a GDM framework, which works in multidimensional environmental space, projected both temporally and spatially.

Invertebrates are often used to monitor ecological change in terrestrial ecosystems because of their critical roles in ecosystem function and dominant contribution to faunal diversity (McGeoch, 1998). Ants are particularly commonly used in environmental assessments,

due to their ecological dominance and sensitivity to environmental change (Andersen, Fisher, Hoffmann, Read, & Richards, 2004; Andersen & Majer, 2004; Underwood & Fisher, 2006). Patterns of diversity and composition in ant communities are strongly related to climatic variables such as temperature, precipitation and humidity (Diamond et al., 2012; Dunn et al., 2009; Kaspari, Alonso, & O'Donnell, 2000; Sanders, Moss, & Wagner, 2003). In this study, we apply GDM to a comprehensive dataset for the diverse rain forest ant communities of the Australian Wet Tropics (AWT) to investigate potential impacts of future climate change based on contemporary spatial patterns of compositional turnover.

Our specific aims are to: (a) identify environmental variables that are most correlated with compositional dissimilarity in rain forest ant communities throughout the AWT, using GDM combined with a theoretic approach; (b) use the GDM to forecast changes in the area of climatically suitable habitat for different ant community types; and (c) predictions to

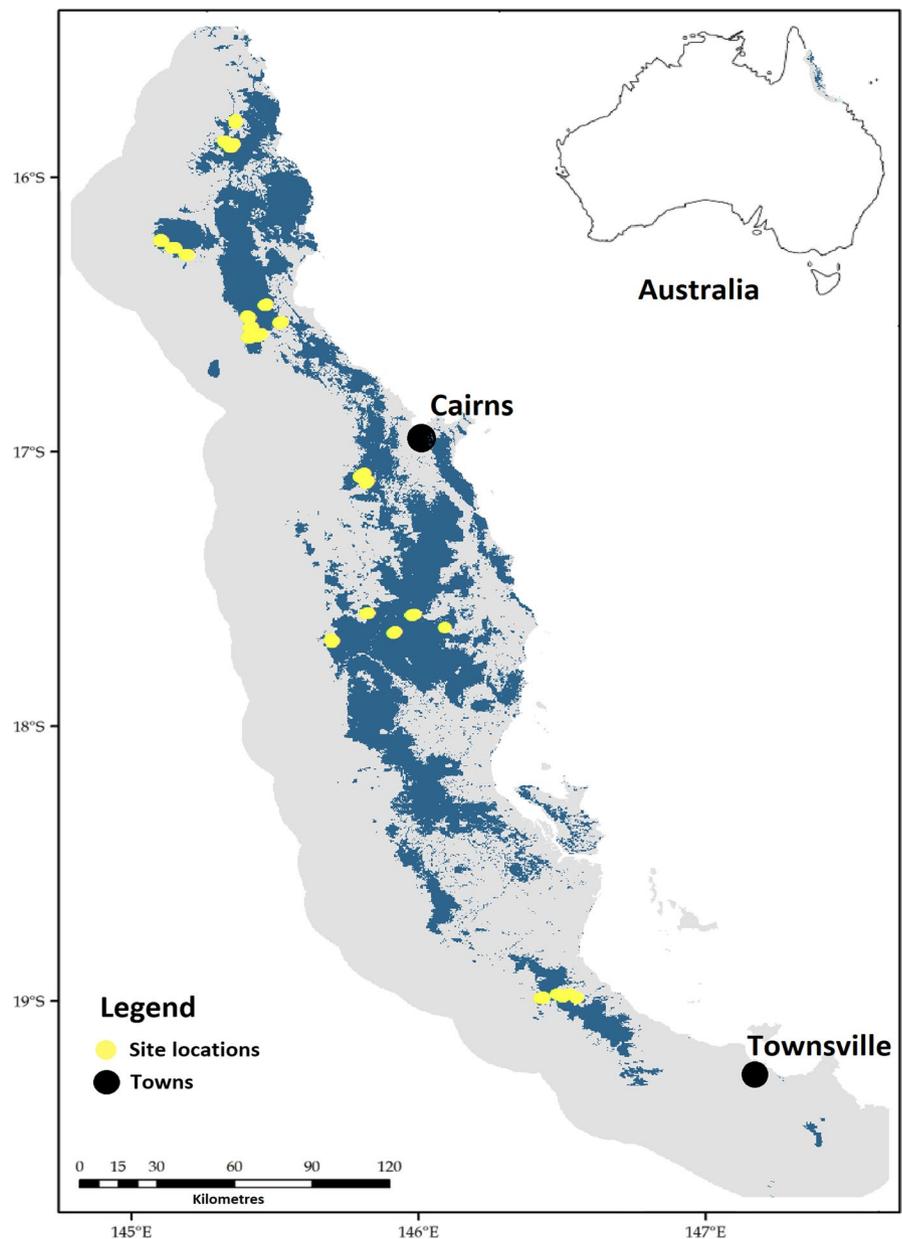


FIGURE 1 The Australian Wet Tropics bioregion with site locations. Dark shade represents the extent of rain forest within the region

account for both the direct effects of climate on ant community changes and the indirect effects of habitat loss on the extent of suitable habitat for the community. Our study will allow the identification of areas in the AWT that are likely to be most sensitive to climate change impacts and are therefore priorities for conservation management.

2 | METHODS

2.1 | Study sites and compositional data

Mean annual rainfall in the AWT (Figure 1) varies from about 1,500–9,000 mm, with 75%–90% occurring between November and April (McDonald & Lane, 2000). Within the region, mean temperature declines at a rate of about 1°C for every 200 m increase in elevation (Shoo, Williams, & Hero, 2005a). Our study was confined to rain forest and covered a range of structural rain forest types from complex mesophyll vine forest in the fertile lowlands to upland simple notophyll vine forest (Adam, 1992; Hilbert, 2008).

Despite their relatively small area, the AWT rain forests are recognized as a major biodiversity hotspot of global significance due to their extraordinary biological richness and biogeographical uniqueness (Zachos & Habel, 2011). However, this biodiversity is highly threatened by anthropogenic climate change (Hilbert, Ostendorf, & Hopkins, 2001; Ostendorf, Hilbert, & Hopkins, 2001; Suppiah, Macadam, & Whetton, 2007; Thomas, Cameron, Green, & Bakkenes, 2004). The rain forests are predicted to decrease in extent by 60% with a temperature rise of 1°C combined with a 10% decrease in precipitation (Hilbert et al., 2001). Future projections show significant decreases in core distributional area of all 65 endemic vertebrates (Williams et al., 2003) and in population size of 74% of rain forest birds (Shoo, Williams, & Hero, 2005b). The insects of the AWT are also highly threatened by climate change, with predictions of the extinction of a large proportion (40%) of schizophoran flies (Wilson, 2010), and 88% reduction in population size of flightless ground beetles (Staunton, Robson, Burwell, Reside, & Williams, 2014).

We used a recent dataset of 5,204 occurrence records of 296 ant species comprehensively sampled using bait traps on the ground and tree trunks, litter extractions and pitfall trapping from 150 sites that cover the full latitudinal and elevational range of rain forest in the AWT (Nowrouzi et al., 2016). A combination of techniques was used to target the distinct faunas associated with litter (cryptic species), the litter surface (epigaeic species) and trees (arboreal species) (Bruhl, Gunsalam, & Linsenmair, 1998), with high sampling intensity to provide reliable estimates of species composition (Ashcroft et al., 2010). Rarefaction curves indicated that most species occurring in the region were recorded (Nowrouzi et al., 2016). The sites were distributed across six mountains, ranging from the Finnegan uplands in the north, to Mt Spec in the south, over a distance of approximately 500 km. All sites were located on granite-derived soils except for those in the Atherton sub-region which contains more-fertile basaltic soils (McJannet, Wallace, Fitch, Disher, & Reddell, 2008; Parsons & Congdon, 2008). The elevational range of study sites varied among subregions, due to differences in the availability and accessibility of rain forest habitats. Sampling

transects were separated by 200 m elevation from the lowland rain forests to the upland following the elevation contour, with six sites separated by 200 m along each transect. Only three sites were located at each of the 350 m elevation transect at Mt Spec and 100 m elevation transect at Atherton due to limited rain forest cover. All ants were sorted to species and where possible named through comparison with identified specimens held in the CSIRO Tropical Ecosystems Research Centre in Darwin. Unidentified species were assigned species codes that apply only to this study and highly diverse genera were identified to species group following Andersen (2000).

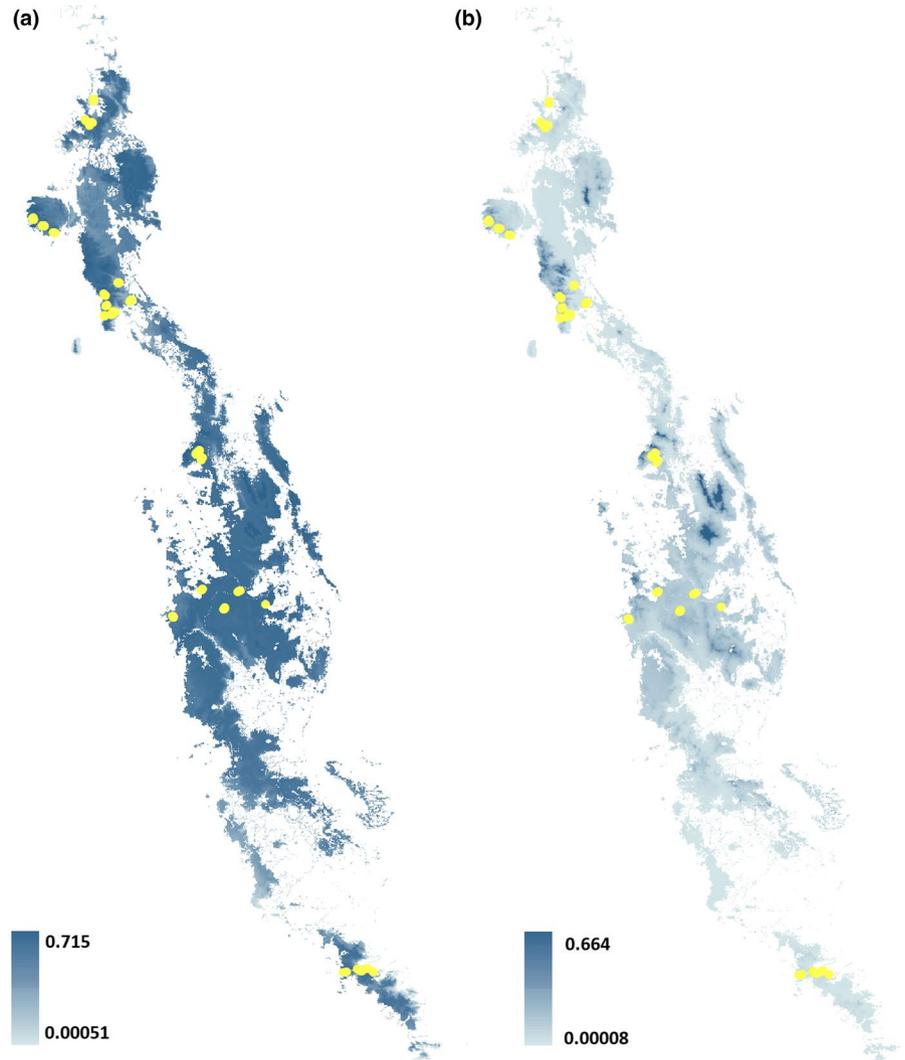
2.2 | Environmental variables, habitat condition and climate projections

We generated a comprehensive set of environmental variables including bioclimatic variables (BC01–BC35), soil and topographic layers, along with information on litter depth, canopy cover and disturbance. Bioclimatic data were used to represent the baseline climate, defined as a 30-year average from 1976 to 2005. These data were derived using the ANUCLIM 6.0 software (Xu & Hutchinson, 2013) at a 9-s resolution, approximately 250-m grids (Hutchinson, Stein, & Stein, 2009). Soil properties were sourced from the Soil and Landscape Grid of Australia, which were based on estimated values from 0 to 5 cm depth and derived from the National Soil Attribute Map as composite products (<http://www.clw.csiro.au/aclep/soilandlandscapegrid>) as well as from the Commonwealth Scientific and Industrial Research Organisation (CSIRO) and the Terrestrial Ecosystem Research Network (TERN), created using terrain analysis techniques developed by Gallant (2000), <http://www.asris.csiro.au/arcgis/rest/services/TERN>. Litter depth, canopy cover and habitat disturbance (tree falls and cyclone damage) were measured during sampling at the sites (Staunton (2013)).

To include the indirect effects of habitat suitability on the community changes, vegetation data were extracted from the National Vegetation Information System broad vegetation subgroups (Australian Government Department of the Environmental Water Resources, 2007). Analyses of future changes in rain forest vegetation were based on a method of habitat condition assessment that integrates remotely sensed rain forest vegetation layers and available field-based reference data to assign each 250 × 250 m cell a habitat condition value (*h*) ranging from 0 (totally unsuitable for rain forest species) to 1 (capable of supporting the maximum number of plant species) (Harwood et al., 2016). A previous analysis has assigned habitat condition values to AWT rain forest currently ranging from 0.001 to 0.715, and maximum values are restricted to forests of previous climates, with higher values occurring in mountain ranges dominated by complex notophyll vine forests, and lowest values occurring in low lands dominated by sclerophyll open forest and savanna woodland (Figures 2a and 3a).

Future projections of climatic data were extracted from 30-year averages of bioclimatic layers within three different times, 2035, 2055 and 2085. These layers were applied as splined deltas over the 9-s resolution environmental layers. We used the Australian Climate Futures Tool (<http://www.climatechangeaustralia.gov>).

FIGURE 2 Current habitat condition of the rain forest in the AWT (a) and a projection in future (b, MIROC 2085). Darker colour represents higher-condition habitats in terms of capacity to support the maximum number of plant species. Site locations are presented for clarity



au/en/climate-projections/climate-futures-tool/), which has been built on Climate Futures Framework (Clarke, Whetton, & Hennessy, 2011; Whetton, Hennessy, Clarke, McInnes, & Kent, 2012) to select the climatic models. This tool includes projections from global and regional climate models based on simulations performed

for the Intergovernmental Panel on Climate Change (IPCC) Fifth Assessment Report (Pachauri et al., 2014). We selected 2 out of 15 global climate models that best reproduced Australian average (1961–1990) patterns of temperature and rainfall (Suppiah et al., 2007): (a) “mild” (Model for Interdisciplinary Research on Climate

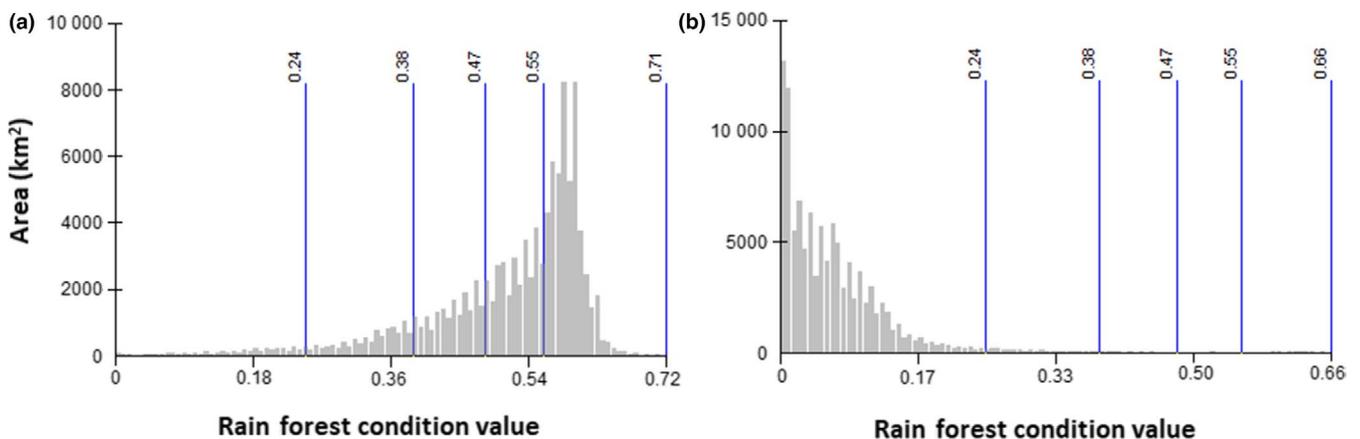


FIGURE 3 Profile of condition values for AWT rain forest habitat under the current climate (a) and a 2085 projection, MIROC (b)

(MIROC -H; ~125 km resolution) and (b) “harsh” (Geophysical Fluid Dynamics Laboratory [GFDL] 2.0; ~300 km resolution), under the greenhouse gas concentration RCP8.5 scenario. Future projections of rain forest condition were also extracted from SDMs of projected rain forest vegetation layers that were derived using the ANUCLIM 6.0 software (Xu & Hutchinson, 2013) at a 9-s resolution and 250-m grids (Hutchinson et al., 2009), provided by eResearch Centre, James Cook University, Australia.

2.3 | Analyses

2.3.1 | Environmental predictors of compositional dissimilarity

We first selected 17 out of 28 environmental (19 bioclimatic, six soil and three habitat) variables using Pearson correlation coefficients to exclude highly correlated variables in the dataset (Table A1). We then assessed which environmental variables best explained dissimilarity of ant communities across the sample sites using the variable selection strategy detailed in Williams et al. (2010) and GDM (Ferrier et al., 2007). This strategy ranks the variables based on their “explained deviance” in the model and selects the best predictors (which reduced the number of variables to 9 out of 17 in this study). To increase the certainty of our variable selection, we also assessed them by using an information-theoretic approach (Burnham & Anderson, 2002). This approach fits multivariate Generalized Linear Models (GLMs) for species composition, developed by Wang, Naumann, Wright, and Warton (2012), using the nine selected predictors. We used a model averaging technique that quantifies relative importance (likelihood) of all possible models that can be generated using the combinations of selected predictor variables ($2^9 = 512$ models in this study case), based on a modified Akaike Information Criterion (AICc). We then evaluated the standardized effect size of each predictor variable by calculating the differences between observed summed Akaike weight and mean summed Akaike weight derived from 999 null datasets, divided by the standard deviation of summed Akaike weights of null datasets. The calculations were all executed using the *mglnm* R package developed by Katabuchi and Nakamura (2015). When using the information-theoretic approach, we did not directly include geographic distance as a variable because of correlation between climatic variables (e.g., temperature) and geographic location (e.g., latitude and elevation). However, as excluding geographic distance did not change the impact of other variables in the model, we included it as a driver of composition turnover in the model as suggested by Williams et al. (2010).

2.3.2 | Compositional change under future climates

The selected environmental factors were used as covariates in a GDM fitted using a matrix of pairwise dissimilarities in ant species composition among the 150 locations sampled. Dissimilarity was calculated using the Sørensen index (Roberts et al., 2017).

The GDM assumes that the amount of change in species composition expected for any location as a result of climatic change will be equivalent to the compositional dissimilarity currently observed between that location and another location with a current climate matching that projected for the first location (Ferrier, Harwood, & Williams, 2012; Ferrier et al., 2007). Predictions of the community's compositional change were obtained by using the model to transform future climate layers as described below. Analyses were conducted using the *ecodist* and *GDM* R packages (Manion, Lisk, Ferrier, Nieto-Lugilde, & Fitzpatrick, 2015; R Development Core Team, 2010).

To address how climate change would affect the rain forest ant communities at different locations, GDM was used to calculate the effective area of similar ecological environments (SEEs), first considering just the direct impacts of climate change, and then also incorporating future changes in vegetation. SEE is a measure of the total area with an environment similar to that of a particular location, scaled according to the rate of biological turnover, and therefore suitable for the local community. The GDM thus transforms maps of environmental predictors into units of ecological distance (ΔE), which are logarithmically related to compositional similarity ($s_{ij} = e^{-\Delta E_{ij}}$) (Allnutt et al., 2008; Ferrier et al., 2012). We then used the stack of transformed grids to examine the predicted compositional similarity (s_{ij}) between current grid cells (i) and points in future scenarios (j) separated over space and time (Allnutt et al., 2008).

The similarity of each current cell was compared to 10,000 points under future climate scenarios to calculate the change in area of SEE (C_i) considering only the direct effects of climate change on the ant community (i.e., regardless of any potential changes in rain forest vegetation):

$$C_i = \frac{\sum_{j=1}^{j=n} s_{ji}^{\text{future}}}{\sum_{j=1}^{j=n} s_{ji}^{\text{current}}} \quad (1)$$

To incorporate vegetation condition in SEE calculations, we repeated each calculation after layers estimating rain forest habitat condition (Harwood et al., 2016) were overlaid on the transformed grids from GDM. Based on the model of ant turnover, the effective area of habitat that is currently ecologically similar, A_i , was calculated for each rain forest cell:

$$A_i = \sum_{j=1}^n s_{ij} h_j \quad (2)$$

To incorporate the current habitat suitability into direct impact of climate change on the ant communities, we repeated the calculations by overlapping the layers of current rain forest habitat condition and the transformed GDMs of the ant communities according to future

TABLE 1 Sum of the coefficients based on the GDM results, ranking the relative strength of the environmental variables contributing to dissimilarity of ant species composition

Variable	Coefficient
Geographic	
Geographic distance	0.47
Climatic	
Isothermality	0.15
Temperature seasonality	0.41
Mean temperature of warmest Quarter	0.52
Mean temperature of coldest Quarter	0.66
Precipitation of wettest period	0.16
Soil	
Bulk density of soil	0.73
Available water capacity of soil	0.20
Site context	
Litter depth	0.05
Habitat disturbance	0.19
Model explanation	25.78

Values in bold represent the greatest explanatory variables.

climate projections and calculated the proportional reduction in SEE within the current condition of rain forest habitat using the equation:

$$C_i = \frac{A^{\text{future climate}}}{A^{\text{current climate and habitat}}} \quad (3)$$

To indicate the overall impact of climate change on ant communities, considering its direct impact combined with indirect effects through changes in rain forest habitat, we overlapped the projected rain forest habitat condition layers and the transformed GDMs according to future climate projections and calculated the proportional reduction in SEE within the “changing rain forest” using the equation:

$$C_i = \frac{A^{\text{future climate and habitat}}}{A^{\text{current climate and habitat}}} \quad (4)$$

Similarly, we calculated the proportion of species retained in the entire rain forest of the region as $P_i = [A^{\text{future climate \& habitat change}} / A^{\text{current}}]^z$ (using z , the exponent of the species–area curve, which is typically 0.25 (Allnutt et al., 2008) and therefore estimate regional species loss. Calculations and projections were conducted using the NET GD Modeller software version 3.1 (Manion, 2014) and GDM R packages (Manion et al., 2015).

3 | RESULTS

3.1 | Environmental predictors of compositional dissimilarity

Nine out of 17 candidate explanatory variables (Table A2) were selected as best explaining the turnover in species composition of ant communities using both GDM and information-theoretic approaches. The GDM accounted for 25.8% of the deviance in observed turnover, and it indicated that environmental and geographic distances both played important roles in explaining compositional dissimilarity (see the sum of the fitted coefficients for each environmental predictor, Table 1). The greatest turnover was explained by the gradient of soil bulk density (BD), followed by mean temperature of coldest quarter (MTCQ), mean temperature of warmest quarter (MTWQ), geographic distance and temperature seasonality (TS) (Table 1). The information-theoretic approach also suggested that turnover could be explained by isothermality, TS, MTWQ, MTCQ, precipitation of wettest period, BD, available water capacity of soil, litter depth and habitat disturbance (Table 2). In contrast to the GDM, the highest effect sizes (>20) were achieved by MTWQ and MTCQ when using the information theory (Table 2).

TABLE 2 Summary results of the information-theoretic approach for identifying predictors of ant species composition, showing (a) summed Akaike weights from observed data, (b) mean summed Akaike weights from randomized data, (c) standard deviation (SD) of summed Akaike weights, standardized effect size ((a-b)/c) and p values calculated from 999 null models generated by permutation

Environmental variable	(a) Summed Akaike weight (observed)	(b) Mean summed Akaike weight (null models)	(c) SD of summed Akaike weight (null models)	Standardized effect size	p value
Isothermality	0.44	0.33	0.02	4.8	0.000
TS	0.52	0.33	0.02	11.2	0.000
MTWQ	0.59	0.33	0.01	23.2	0.000
MTCQ	0.59	0.33	0.01	21.2	0.000
PWP	0.57	0.34	0.02	11.4	0.000
BD	0.50	0.33	0.02	9.4	0.000
AWC	0.51	0.33	0.02	8.2	0.000
Litter depth	0.46	0.33	0.02	6.5	0.000
Habitat disturbance	0.58	0.33	0.02	14.9	0.000

Abbreviations: AWC, available water capacity of soil; BD, bulk density of soil; MTCQ, mean temperature of coldest quarter; MTWQ, mean temperature of warmest quarter; PWP, precipitation of wettest period; TS, temperature seasonality.

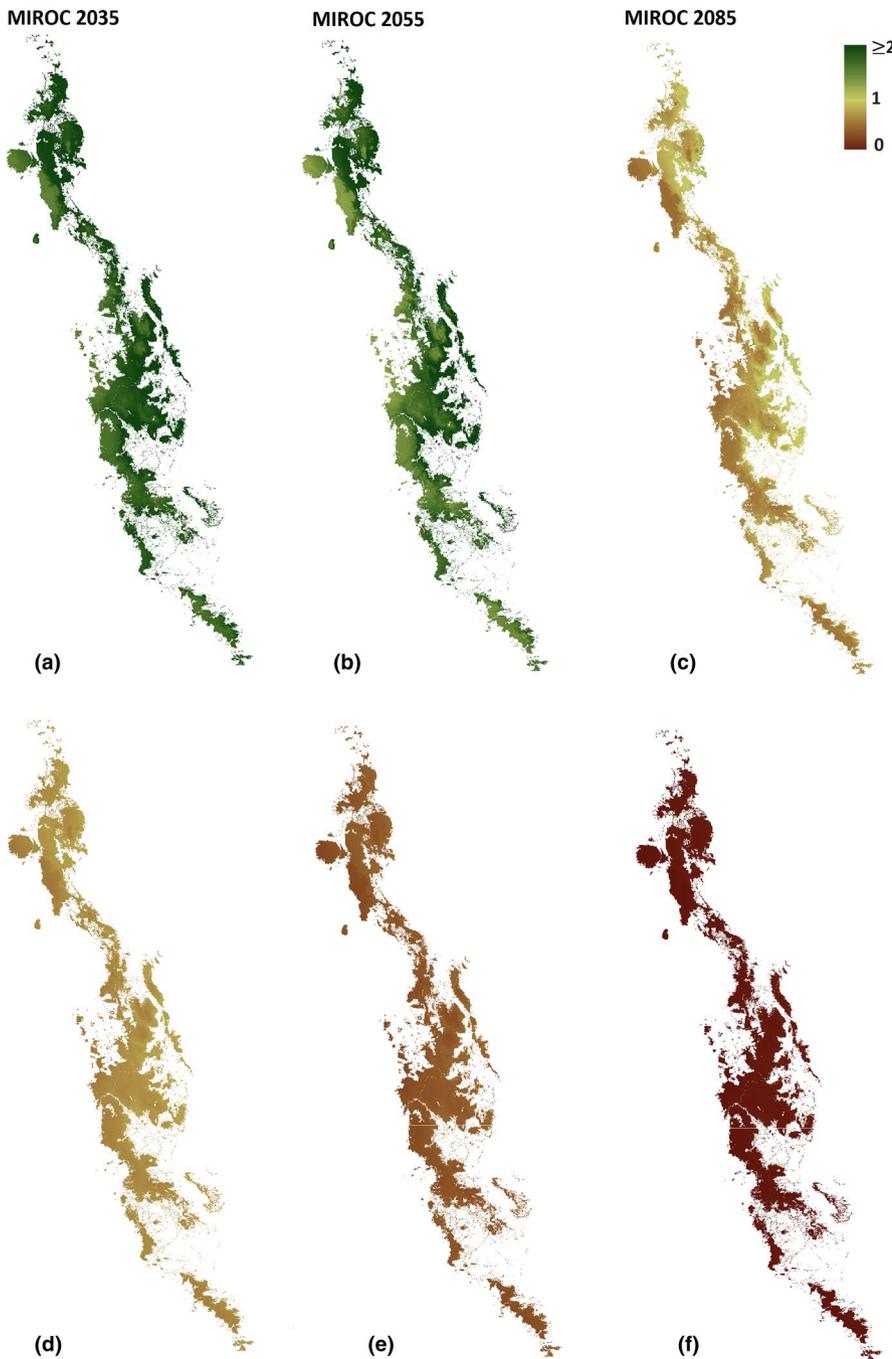


FIGURE 4 Effective area of SEE (similar ecological environment; C value; Equation 3) for predicted ant species composition in the AWT; based on MIROC model within three different times, 2035, 2055 and 2085 (30 years averaged each period; under RCP8.5 scenario); a, b & c: under predicted climate change only; d, e & f: under predicted climate and habitat changes. C value = 1, no change, C value <1, decrease and >1, increase in area of SEE

3.2 | Compositional change under future climates

3.2.1 | Direct effects of climate

Under a mild climate model (MIROC), GDM predicted that the effective habitat area was largely maintained and even increased (particularly in coastal regions) up to 2055 (Figure 4a,b). However, by 2085 the extent of suitable habitat for ant communities had declined by >85%, and 50% of the rain forest ants would lose more than half of their SEE, with the declines occurring primarily inland (Figure 4c; Table 3). Under the harsher GFDL climate model, at least 60% of the communities in the region were predicted to lose more than half of

their SEE by 2085, with only some coastal areas remaining essentially unchanged (Figure 5c; Table 3).

3.2.2 | Incorporating indirect effects of changes in habitat suitability

When changes in habitat suitability are incorporated, >90% of the current rain forest, with higher suitability values of 0.3–0.65 (Figures 2a and 3a), is projected to transition to categories lower than 0.2 by 2085 under MIROC (Figures 2b and 3b). Our modelling indicates that this will result in almost all ant communities in the region experiencing a reduction in their similar habitats (Figures 4 and 5; Table 3).

Over 90% of ant communities were projected to lose more than half their current SEE from (Figures 4f and 5f; Table 3). However, despite the major turnover of ant composition at local scales, only 9 (3%) species were predicted to be lost from the AWT as a region under both climate models when habitat suitability was incorporated.

4 | DISCUSSION

Our study represents the first analysis of climate change impacts on ant communities using comprehensive compositional data and macroecological models. It is also the first study to integrate climate-induced changes in habitat suitability into future projections of a diverse invertebrate group. Both the GDM and information-theoretic approaches indicated that temperature is the most important climatic driver of compositional change in rain forest ant species in either dry (lower temperature) or wet (higher temperature) seasons of the year in the AWT. This result reinforces results from previous studies showing temperature to be a primary driver of ant species diversity patterns, both at global and regional scales (Andersen, 1995; Bishop, Robertson, Rensburg, & Parr, 2014; Diamond et al., 2012; Dunn et al., 2009).

After temperature, habitat disturbance had the second highest effect on dissimilarity of community composition according to the information-theoretic models, and it significantly contributed to the spatial patterning in the GDM. A common effect of habitat disturbance is simplification of habitat structure (Gibb & Parr, 2013; Hoffmann & Andersen, 2003), so disturbance can have especially strong effects in complex habitats like tropical rain forest (Andersen, 2018). Climate change is predicted to increase the frequency of extreme weather events (Williams et al., 2003), including cyclones, which are the major agent of disturbance in the AWT.

Based on our models, 50%–60% of the ant communities across the AWT will likely lose more than half of their SEEs when considering just the direct impacts of climate change. Regardless of differences among the climate models, this increases to >90% when changes in habitat suitability are also incorporated. Such a finding is

consistent with the greater magnitude of projected changes in ant community assemblages compared with that of plants reported by Caddy-Retalic et al. (2018). Thus, projections based on only direct effects of climate change can significantly underestimate the expected changes in ant communities.

Most ant communities currently occurring in the AWT's coastal zone are projected to continue to do so over the next few decades. Coastal ant communities are expected to be buffered from the effects of climate change in the near future due to the close proximity of their habitat to the ocean, which has a moderating influence on temperatures (Dowdy, Abbs, & Bhend, 2015). However, a high degree of turnover in ant composition is expected to occur by 2085 even in coastal areas due to the effects of rising temperatures and altered rainfall patterns on rain forest vegetation. Faster and greater impacts can be expected inland of the mountain ranges, where changes in rainfall and temperature will be more severe (Hughes, 2003; Reside et al., 2013; Suppiah et al., 2007; Welbergen et al., 2015). Throughout much of this region, rain forest is expected to convert to savanna, which is entirely unsuitable for specialist rain forest species. Our analyses of forest conditions are unable to differentiate changes in habitat suitability due to transition within rain forest from those due to the conversion of rain forest to savanna. However, up to 90% of current rain forest in the AWT is expected to convert to sclerophyll open forest and savanna woodland by 2085 (Hilbert, Graham, & Hopkins, 2007; Mokany, Westcott, Prasad, Ford, & Metcalfe, 2014).

Some major uplands and mountain peaks of the AWT, including the Windsor, Carbine and Atherton uplands, have maintained complex notophyll vine forests throughout the Pleistocene (Hilbert et al., 2007) and represent key refugia for rain forest flora and fauna (Reside et al., 2013; Welbergen et al., 2015). These uplands support many endemic ant species; for example, 11 ant species are known only from Carbine uplands (Nowrouzi et al., 2016). Our models reinforce the high sensitivity of these uplands to future climate change (Hilbert et al., 2001; Mokany et al., 2014), particularly those further inland such as Windsor and Carbine. It is highly

TABLE 3 Proportion of modelled changes in ant communities' SEE throughout the AWT, under two climate projections, MIROC (mild) and GFDL (harsh), for the three years (2035, 2055, 2085)

Projections of direct (climate) and indirect (habitat) effects of climate change	MIROC 2035	MIROC 2055	MIROC 2085	GFDL 2035	GFDL 2055	GFDL 2085
Direct effects						
Proportion of area with increase in SEE (%)	>80%	>60%	>5%	>30	10	>5
Proportion of area with decline in SEE (%)	0	<10%	>85	>35%	>55%	>85
Proportion of area losing $\leq \frac{1}{2}$ of SEE- areas with C values >0.5 (%)	0	0	>50	0	0	60
Combined direct & indirect effects						
Proportion of area with increase in SEE (%)	0	0	0	0	0	0
Proportion of area with decline in SEE (%)	~100	100	100	~90	100	100
Proportion of area losing $\leq \frac{1}{2}$ of SEE- areas with C values >0.5 (%)	0	>60	>90	0	~50	>90

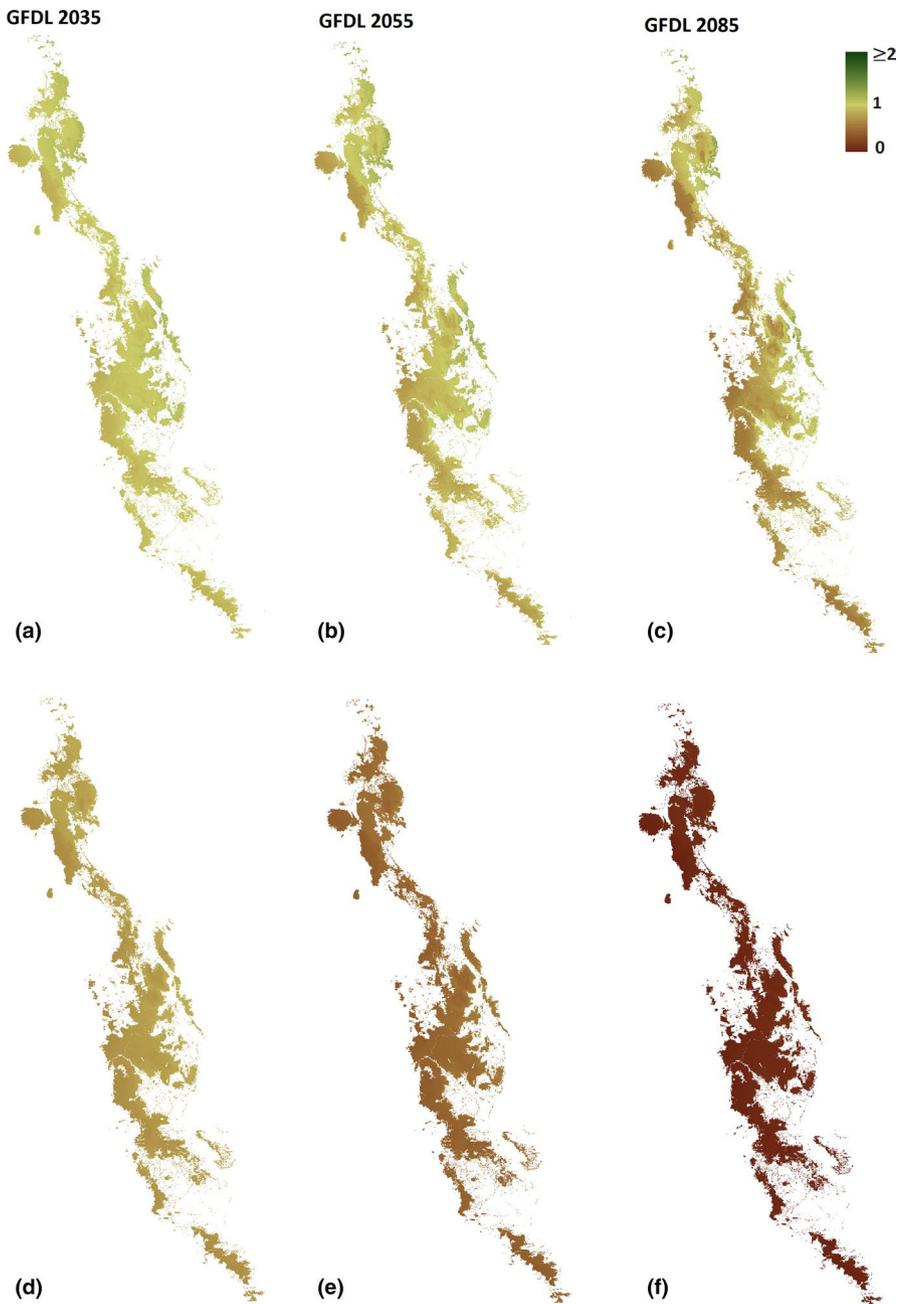


FIGURE 5 Effective area of SEE (similar ecological environment; C value; Equation 4) for predicted ant communities' composition in the AWT; based on GFDL model within three different times, 2035, 2055 and 2085 (30 years averaged each period; under RCP8.5 scenario); a, b & c: under predicted climate change only; d, e & f: under predicted climate and habitat changes. C value = 1, no change, C value <1, decrease and >1, increase in area of SEE

unlikely that such inland refugia will be maintained under future climates.

Our modelling indicates that even with changing rain forest condition, sufficient suitable habitat will remain at the regional level to avoid high extinction rates even under an extreme climate scenario. However, our analyses of compositional change based on SEEs can be considered conservative because it does not account for dispersal limitations. In particular, new SEEs on different mountains might not be accessible for some species, especially for those without winged reproductive, such as within *Lioponera* and *Pseudoneoponera* (Peeters & Ito, 2001). Our analyses also do not account for other factors that can affect extinction rate, such as interactions within metapopulations (Morrison, 2002) and allee effects (Luque, Giraud, & Courchamp, 2013). Additionally, our

models do not consider the potential increased incidence of habitat disturbance through cyclones, which will potentially have a major impact on rain forest suitability, including through increased risk of weed invasion (Turton, 2012).

In conclusion, our study has demonstrated that rain forest ants in the AWT are likely to be severely impacted under climate change. The direct impact of a changing climate is likely to be substantial, as has been concluded for well-studied groups such as birds, reptiles, mammals, frogs, butterflies and dragonflies (Bush et al., 2014; Shoo et al., 2005b; Williams & Pearson, 1997; Williams, Williams, Alford, Waycott, & Johnson, 2006). However, the changes in ant communities can be expected to be far more profound when changes in habitat suitability are also considered. Our study shows that projections of reduction in ecological

environments of ant communities and consequent species turnover in the AWT would be underestimated by 30%–40% without integrating the extent to which their habitat will change under a changing climate. While these findings relate to ant communities, they suggest that modelling of other taxonomic groups, based solely on direct effects, may similarly underestimate the impacts of climate change. The integration of habitat changes in future climate models is likely to substantially improve projections for fauna more generally.

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DATA ACCESSIBILITY

Data for this study will be available on request and may be found through James Cook University library (<https://doi.org/10.4225/28/5ac2fba61317f>).

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APPENDIX

TABLE A1 Pearson correlation coefficients (bottom left triangle) and *p* values (top right triangle) of the 17 environmental predictor variables

	Isothermality	Temperature seasonality	Mean temperature of warmest Quarter	Mean temperature of coldest Quarter	Precipitation of wettest period	Precipitation seasonality	Annual mean radiation	Annual mean moisture index	Precipitation- evaporation ratio	Topographic wetness index	Historical rain forest shift	Aspect	Slope	Available water capacity of soil	Bulk density of soil	Soli clay layer	Soil density
Isothermality	0.000	0.000	0.000	0.000	0.407	0.024	0.025	0.051	0.653	0.079	0.000	0.008	0.001	0.645	0.011	0.804	0.259
Temperature seasonality	0.55	0.000	0.000	0.000	0.508	0.309	0.329	0.000	0.817	0.441	0.055	0.147	0.000	0.639	0.004	0.122	0.026
Mean temperature of warmest Quarter	-0.05	-0.29	0.000	0.000	0.780	0.002	0.032	0.000	0.002	0.014	0.571	0.002	0.809	0.044	0.000	0.000	0.000
Mean temperature of coldest Quarter	-0.28	-0.66	0.91	0.91	0.947	0.003	0.210	0.000	0.019	0.024	0.688	0.086	0.161	0.174	0.000	0.000	0.000
Precipitation of wettest period	0.04	0.06	0.02	-0.01	0.000	0.000	0.000	0.000	0.000	0.097	0.000	0.845	0.030	0.357	0.280	0.000	0.000
Precipitation seasonality	-0.41	-0.08	0.26	0.24	-0.52	0.000	0.000	0.000	0.000	0.046	0.000	0.000	0.042	0.132	0.000	0.000	0.000
Annual mean radiation	-0.13	0.08	0.18	0.10	-0.60	0.70	0.000	0.000	0.000	0.149	0.000	0.000	0.075	0.264	0.001	0.000	0.000
Annual mean moisture index	0.33	0.33	-0.46	-0.51	0.73	-0.87	-0.69	0.000	0.000	0.310	0.000	0.016	0.100	0.056	0.000	0.000	0.000
Precipitation- evaporation ratio	0.04	-0.02	-0.26	-0.19	0.89	-0.77	-0.73	0.89	0.89	0.187	0.000	0.067	0.003	0.035	0.000	0.000	0.000
Topographic wetness index	0.12	-0.06	0.20	0.19	0.14	-0.16	-0.12	0.08	0.11	0.19	0.019	0.608	0.006	0.000	0.018	0.269	0.011
Historical rain forest shift	0.67	0.16	0.05	-0.03	0.35	-0.84	-0.55	0.63	0.48	0.19	0.002	0.002	0.444	0.307	0.800	0.000	0.001
Aspect	0.09	-0.12	-0.25	-0.14	-0.02	-0.30	-0.46	0.20	0.15	0.04	0.25	0.153	0.990	0.017	0.000	0.000	0.037
Slope	0.13	0.30	0.02	-0.12	-0.18	0.17	0.15	-0.14	-0.24	-0.23	-0.06	-0.12	0.000	0.894	0.000	0.000	0.001
Available water capacity of soil	-0.01	-0.04	-0.17	-0.11	0.08	-0.12	0.09	0.16	0.17	0.31	-0.08	0.00	-0.47	0.115	0.000	0.000	0.000
Bulk density of soil	-0.05	-0.24	0.89	0.80	-0.09	0.32	0.27	-0.51	-0.34	0.19	-0.02	-0.20	0.01	-0.13	0.000	0.000	0.000
Soli clay layer	0.25	0.13	-0.58	-0.51	0.49	-0.80	-0.59	0.85	0.76	0.09	0.48	0.34	-0.29	0.40	-0.60	0.000	0.000
Soil density	0.15	0.18	-0.70	-0.63	0.43	-0.59	-0.39	0.76	0.66	0.21	0.27	0.17	-0.27	0.49	-0.72	0.83	0.83

TABLE A2 Pearson correlation coefficients (bottom left triangle) and *p* values (top right triangle) of the nine predictor variables selected by the models

	TS	MTWQ.	MTCQ.	PWP	BDW	AWC	Isothermality	Litter depth	Disturbance
TS		0.002	0.577	0.656	0.256	0.116	0.000	0.009	0.045
MTWQ	-0.26		0.000	0.476	0.859	0.000	0.001	0.000	0.000
MTCQ	-0.05	0.78		0.780	0.002	0.587	0.000	0.001	0.000
PWP	0.04	0.06	0.02		0.845	0.016	0.023	0.000	0.000
BDW	0.09	0.01	-0.25	-0.02		0.099	0.010	0.107	0.370
AWC	0.13	-0.29	-0.05	-0.20	-0.14		0.644	0.000	0.110
Isothermality	0.55	0.04	-0.28	0.04	-0.05	-0.01		0.000	0.000
Litter depth	-0.22	-0.34	-0.28	-0.43	-0.13	0.34	0.74		0.000
Disturbance	0.17	0.31	0.52	0.54	-0.07	-0.13	-0.69	-0.58	