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Ant thermal tolerances under climate, land cover and land use change

Nigel R Andrew Corresp., [1, 2] , **Cara Miller** [3] , **Graham Hall** [2] , **Zac Hemmings** [1, 2] , **Ian Oliver** [2, 4]

[1] UNE Centre of Excellence for Behavioural and Physiological Ecology, Natural History Museum, University of New England, Armidale, NSW, Australia
[2] School of Environmental and Rural Science, University of New England, Armidale, NSW, Australia
[3] School of Science and Technology, University of New England, Armidale, NSW, Australia
[4] Office of Environment and Heritage, Armidale, NSW, Australia

Corresponding Author: Nigel R Andrew
Email address: nigel.andrew@une.edu.au

Thermal stress is a key issue for species dominant within ecosystems especially those that carry out key ecosystem service roles. When assessing the impacts of climate change it is critical to assess its biotic impacts relative to other anthropogenic changes to landscapes including the reduction of native vegetation cover, landscape fragmentation and changes in land use intensity. Here we integrate the observed phenotypic plasticity of the dominant and ubiqitous meat ant *Iridomyrmex purpureus* in critical thermal limits across altitudinal, land cover and land use gradients to: (i) predict the adaptive capacity of a key terrestrial ecosystem service provider to changes in climate, land cover and land use, and (ii) assess the ability of multiple use landscapes to confer maximum resilience to terrestrial biodiversity in the face of a changing climate. The research was carried out along a 270km aridity gradient spanning 840m in altitude in northern New South Wales, Australia. When we assessed critical thermal maximum temperatures (CT_{max}) of meat ants in relation to the environmental variables, and within the model we had critical thermal minimums of meat ants (CT_{min}) as a random slope and as a fixed effect we detected a negative aridity effect on CT_{max}, a negative effect of land use intensity, and no overall correlation between CT_{max} and CT_{min}. We also found a negative relationship with warming tolerance of *I. purpureus* and landscape aridity. In conclusion, we expect to see a reduction in the physiological resilience of *I. purpureus* as land use intensity increases and as the climate becomes more arid. Meat ants are key ecosystem engineers and as they are put under more stress, wider ecological implications may occur if populations decline or disappear.

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N. R. Andrew[1, 2], C. Miller[3], G. Hall[2], Z. Hemmings[1, 2], and I. Oliver[2, 4]

[1] UNE Centre of Excellence for Behavioural and Physiological Ecology, Natural History Museum, University of New England, Armidale, NSW, 2351.

[2] School of Environmental and Rural Science, University of New England, Armidale, NSW, 2351.

[3] School of Science and Technology, University of New England, Armidale, NSW, 2351

[4] Office of Environment and Heritage, PO Box U221, Armidale, NSW, 2351

Abstract

Thermal stress is a key issue for species dominant within ecosystems especially those that carry out key ecosystem service roles. When assessing the impacts of climate change it is critical to assess its biotic impacts relative to other anthropogenic changes to landscapes including the reduction of native vegetation cover, landscape fragmentation and changes in land use intensity. Here we integrate the observed phenotypic plasticity of the dominant and ubiqitous meat ant *Iridomyrmex purpureus* in critical thermal limits across altitudinal, land cover and land use gradients to: (i) predict the adaptive capacity of a key terrestrial ecosystem service provider to changes in climate, land cover and land use, and (ii) assess the ability of multiple use landscapes to confer maximum resilience to terrestrial biodiversity in the face of a changing climate. The research was carried out along a 270km aridity gradient spanning 840m in altitude in northern New South Wales, Australia. When we assessed critical thermal maximum temperatures (CT_{max}) of meat ants in relation to the environmental variables, and within the model we had critical thermal minimums of meat ants (CT_{min}) as a random slope and as a fixed effect we detected a negative aridity effect on CT_{max}, a negative effect of land use intensity, and no overall correlation between CT_{max} and CT_{min}. We also found a negative relationship with warming tolerance of *I. purpureus* and landscape aridity. In conclusion, we expect to see a reduction in the physiological resilience of *I. purpureus* as land use intensity increases and as the climate becomes more arid. Meat ants are key ecosystem engineers and as

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Introduction

Assessing the performance and physiological responses of ectotherms is critical to understanding biotic responses to climate change (Andrew & Terblanche 2013), particularly the effects of exposure to thermal stress and temperature extremes (Vasseur et al. 2014) on key ecosystem service providers. Biochemical and physiological reactions are mediated by temperature and thermal stress can negatively influence development, growth, metabolism, movement and reproduction, leading to changes in community and ecosystem level processes (Dell et al. 2011; Grigaltchik et al. 2012). Thermal performance curves identify how the performance or fitness of an ectotherm is influenced by body temperature (Sinclair et al. 2016), a key response to thermal stress identified by these curves are critical thermal limits: the functional endpoint that identify upper and lower limits of temperatures that insects can tolerate from which they are unable to escape (Lighton & Turner 2004).

Thermal stress is a key issue for all taxa including those that provide key ecosystem services and are dominant within ecosystems (Andrew 2013; Andrew et al. 2016; Andrew et al. 2013a; Mooney et al. 2009). Through many terrestrial ecosystems worldwide, ants provide key ecosystem services and mediate key ecosystem processes (Del Toro et al. 2012; Hölldobler & Wilson 1990). The resilience of these ecosystem service providers to thermal stress may change among populations as they are exposed to different environmental conditions, particularly in a more variable climate (Greenslade 1976). This phenotypic (or physiological) plasticity is a core driver of adaptive responses to climatic variation (Kingsolver & Huey 1998).

It is especially critical to take into account the impacts of climate change relative to other anthropogenic changes to landscapes including the reduction of native vegetation cover, landscape fragmentation and changes in land use intensity (Oliver & Morecroft 2014; Sala et al. 2000). Assessing the synergistic effects of changes in land cover, land use and climate are critical to enable decision makers to make better determinations in regards to the management and conservation of biodiversity, ecosystem and environmental services both now and into the future (Mawdsley et al. 2009). Previously we assessed how adapting landscapes may improve insect biodiveristy conservation via a study of the additive and synergistic effects of climate with land cover and land use change (Oliver et al. 2016). From the main-effects models developed, it was found that a greater amount of woody plant canopy cover increases ant richness (species and genus) and diversity; whereas a higher amount of land cultivation, grazing, exotic plant groundcover and bare ground reduced species richness. At sites with warmer and drier climates (i.e. a higher aridity index), native plant canopy cover had greatest benefit, and exotic plant cover had the most negative effects, on ant species richness (Oliver et al. 2016). From this, we predict that the effects of landscape change on diversity may also affect the thermal physiology of insect populations.

Changes in a dominant and widespread ectotherm’s critical thermal limits across climatic, land use and land cover gradients may occur (Angilletta et al. 2007): leading to changes in community structure and the provision of ecological services (Traill et al. 2010). Exposure to different microclimates may influence ectotherm physiology in more unpredictable ways than just exposure to warmer temperatures individually. Microclimates that ants are exposed to (e.g. Andrew et al. 2013a; Hemmings & Andrew 2017) may change substantially across surfaces within different habitat spaces: such as those with substantive bare ground, a high grazing intensity, exotic plant species cover, and woody ground cover.

Here we focus on meat ants (*Iridomyrmex purpureus* (Smith, F., 1858)) as they are a dominant and ubiquitous part of the landscape (Andersen 2000; Greaves 1971; Greenslade 1976). *Iridomyrmex purpureus* can have a substantive impact on the availability of resources and the use of these resources by other species in different landscapes (Gibb 2005). *Iridomyrmex purpureus* are also excellent at resource exploitation and interference competiton to enable them to dominate and control resources quickly (Gibb & Hochuli 2004). They can also maximise their foraging times by displaying opportunistic thermal responses and adjusting foraging behaviour to deal with high trail temperatures (Andrew et al. 2013a).

Warming tolerance defines how much warming an ectotherm can tolerate before lethal levels are attained (Deutsch et al. 2008): it is calculated by taking the difference between the upper critical thermal limit and the habitat ambient temperature. These values can change substantially based on the method from which habitat temperatures are derived. For example, Andrew *et al.* (2013a) found *I. purpureus'* warming tolerance at a site in temperate Australia (Armidale, New South Wales (NSW)) to be relatively high (25.8°C) when habitat temperatures were based on closest weather station annual averages, but warming tolerance reduced when closest weather station summer average temperatures and then microclimate summer average temperatures were used (19.52°C and 19.12°C respectively). Warming tolerance decreased substantially (to 7.81°C) when microclimate temperatures based on summer temperatures between 10am and 4pm (when ants are most surface active) were used.

In this study we integrate observed ant phenotypic plasticity in critical thermal limits across altitudinal, land cover and land use gradients to: (i) predict the adaptive capacity of terrestrial invertebrate biodiversity to changes in climate, land cover and land use, and (ii) assess the ability of multiple use landscapes to confer maximum resilience to terrestrial biodiversity in the face of a changing climate.

The following questions were addressed:

What were the critical thermal limits (CT_{max} and CT_{min}) for *I. purpureus* across sites representing the main climatic, vegetation, and land-use regimes?

What were the key environmental drivers (climatic, vegetation, and land-use regimes) influencing thermal limits?

What is the relationship between *I. purpureus'* warming tolerance and aridity along the environmental gradient?

Methods

Site selection

The study was carried out along a 270km aridity gradient spanning 840m in altitude in northern NSW, Australia (Table 1). The area has some of the most fertile soils in Australia, with much of the farming practices dominated by livestock grazing on modified pastures and native vegetation, and dryland and irrigated cropping (BRS 2009). Native remnant vegetation is dominated by semi-arid woodlands at lower altitudes through to grassy woodlands and dry sclerophyll forest at higher altitudes (Keith 2004). Eleven sites were chosen to represent a range of climatic, land-use and native woody vegetation cover along this gradient (Table 1) covering the total number of sites (87) that were used to assess ant species diversity (Oliver et al. 2016). Sites were chosen to maximise the range in climate (Aridity: based on rainfall and evaporation collected from modelled climate data from ANUCLIM 6.1 (Xu & Hutchinson 2011) over three time periods: 3 months, 12 months and 36 months), land cover (total native woody cover (Canopy) and bare ground), land use (intensity of use: Land Use Intensity - LUI, and exotic groundcover) and soil pH and clay content. Land use intensity is a semi-quantitative index based on cultivation and grazing severity and age: so more intensively managed sites have higher values (ranging between 0 and 12). More information on how these variables were calculated and justified can be found in Oliver *et al.* (2016).

We used the ant dataset collected from Oliver *et al.* (2016) to identify a common and widespread species to assess for critical thermal limits. *Iridomyrmex purpureus* was chosen for physiological tolerance comparisons as it was the most abundant species at each site. A minimum of 15 individual ants were collected from each site between April and May 2014, and then held at 25°C for two hours to avoid effects of time of day of capture differences along the gradient. Previous work on *I. purpureus* found no effect of time of day of capture/ nest temperature on thermal tolerances (determined via thermolimit respirometry) from a single site (Andrew et al. 2016).

Critical thermal maximum and minimum assessments (CT_{max} and CT_{min})

CT_{max} measurements were carried out in a Grant R4 waterbath with a GP200 heater using distilled water. Ten individuals from each site were each put into a single 50ml vial for testing, and a reading for each ant was taken. Waterbath temperature was initialised for 10 minutes at

25°C and then ramped at 0.25°C/minute until CT_{max} was reached. CT_{max} was identified when an individual ant could not perform coordinated motor functions in the vial to right itself after being turned onto its side (Andrew et al. 2013a). CT_{max} could go up to 55°C (equivalent to 120 minutes/individual – 30°C temperature change at 0.25°C/min). Ramping at 0.25°C is considered the most 'standard' temperature ramping rate, at which the body temperature of ants is in equilibrium with their surroundings (Andrew et al. 2013a; Chown et al. 2009; Lighton & Turner 2004; Nguyen et al. 2014; Terblanche et al. 2007). CT_{min} was carried out in a similar fashion to CT_{max} using 1:1 distilled water/glycol mix. Waterbath temperature was initialised for 10 minutes at 5°C and then decreased at 0.25°C/minute until CT_{min} was reached. CT_{min} was identified when an individual ant could not perform coordinated motor functions in a 50ml vial to right itself after being turned onto its side (Andrew et al. 2013a). CT_{min} could go down to -15°C (equivalent to 80 minutes/species – 20°C temperature change at 0.25°C/min). To measure temperatures that ants were exposed to within each vial, a Type-T thermocouple was placed within another 50ml vial that was plunged with the ants and connected to a temperature datalogger (Testo 175 T3) with data logged as waterbath temperatures were ramped: the Testo temperature was used to identify ant $CT_{max/min}$.

Model fitting

We used *R* (R Core Team 2017) and the R package *lme4* (Bates et al. 2015) to perform a linear mixed effects analysis of the relationship between CT_{max} as a response variable against the environmental variables of aridity, LUI (converted to a proportion), soil clay content, exotic plant ground cover, and total native woody cover (Canopy) designated as fixed effects. We explored singular interaction effects of Aridity:LUI, Canopy:LUI, and Clay:LUI in some models as well as the impact of dropping main effect variables. With this framework we considered random intercept models by site only, and by both site and CT_{min} (individually). We also considered a random intercept, random slope model with CT_{min} within Site as the random effect. We repeated this model selection process with CT_{min} as the response variable and CT_{max} as the predictor variable where appropriate. All variables were centred and scaled. Models were initially fit with REML and then refitted with ML for comparison in Likelihood ratio tests.

Minimum AIC values and p-values of less than 0.05 were used to aid model selection. Visual inspection of residual plots of the preferred models were used to assess obvious deviations from homoscedasticity or normality. Visualization of random effects were undertaken using R package *sjPlot* (Lüdecke 2017). Standard errors and confidence intervals for predicted values of preferred models were undertaken using parametric bootstrapping (n = 1000) within R package *bootpredictlme4* (Duursma 2017) and visualized within R package *visreg* (Breheny & Burchett 2017).

Warming Tolerance

Warming tolerance was calculated using the equation of Deutsch *et al.* (2008) and Diamond *et al.* (2012): CT_{max} - T_{hab}. The T_{hab} calculation may include different calculations (e.g. annual average; summer average; microclimate summer average; and microclimate summer 10am-4pm summer average) which are ecologically relevant and to identify the most appropriate to assess ectotherm stress (e. g. Andrew et al. 2013a). For T_{hab} here, we did not have access to microclimate data, so we modelled site location data using ANUCLIM V6.1 (Xu & Hutchinson 2011) from the closest weather stations based on 3 month summer average 2009, 12 month average for 2009 and 36 month (2007-2009) average day temperatures. These weather data were used, as the data were generated for all sites at the time of sampling ant species richness in Oliver *et al.* (2016).

Results

Critical thermal maxima of individual ants ranged between 41.5°C and 56.1°C, and CT_{min} between 0.3°C and 7.1°C in this study. There was no consistent relationship between CT_{min} and CT_{max} across the 11 sites sampled (Figure 1), suggesting no causal relationship between the two end points.

The preferred model proposed for explaining meat ants CT_{max} across the landscape is:

CT_{max} ~ LUI + Canopy + Exotic + Clay + Aridity + (CT_{min}|SITE_ID)

The fixed effects for this model are shown in Table 2. The overall random effects for the model above are (in terms of variance): Site: 1.0448; CT_{min}|Site: 0.1937; and Residuals: 1.4886. As shown in Figure 2, Sites are an important source of variation (much more so than CT_{min} although the inclusion of this was still significant as per the model selection process). However, there is still additional (unaccounted for) variation in the residuals. For the variables of LUI and Clay, there were significant relationships with CT_{max} (Figure 3). As LUI increases, CT_{max} decreases; whereas clay content was positively correlated with CT_{max}.

For explaining meat ants CT_{min} across the landscape a similar model is proposed as that for CT_{max}:

CT_{min} ~ LUI + Canopy + Exotic + Clay + Aridity + (CT_{max}|SITE_ID)

The fixed effects for this model are shown in Table 3. The overall random effects for the model above are (in terms of variance): Site: 1.3011; CT_{max}|Site: 0.3484; Residuals: 1.3769. As with CT_{max}, the sites also exhibit a high amount of variation (Figure 2). The prediction intervals for CT_{min} also show similar results as those for CT_{max}, (Figure 3c and d) however the relationships are weaker for both LUI and Clay content.

We found a negative relationship between the warming tolerances of *I. purpureus* and landscape aridity (Figure 4). This relationship was consistent among all measures of mean temperatures (no significant difference in Test for Common Slope across Groups: Test Statistic = 1.488, p = 0.482). There was a significant difference in the slope elevation of warming tolerance between the three month and thirty six month mean temperature calculations (Figure 4; d.f. = 2, WALD = 95.299, p < 0.0001).

Discussion

The phenotypic plasticity in critical thermal limits and physiological responses of insects to a changing climate is crucial for understanding how individuals and populations will respond to changes in their local environment (Andrew et al. 2013b; Andrew & Terblanche 2013). These responses are becoming a key area of research interest (Andrew et al. 2013a). The assessment of common species responses to a changing climate needs to be thoroughly assessed, as changes in these taxa's population structure can have large implications for the ecosystems in which they provide key services (Andrew 2013; Gaston 2011; Inger et al. 2014). In addition, as landscapes become more fragmented and anthropogenic, common and dominant species responses to changes may also be limited. Here, critical thermal maxima and minima were determined for ants that encompassed an extensive distribution along an environmental gradient.

There was no strong pattern in CT_{max} and CT_{min} associated with the environmental variables tested. The results of the CT_{max} measurements indicates there is a high variation of CT_{max} across sites, this may be due to the ants being field fresh and so their previous exposure to a variety of stresses may influence their thermal capabilities. However, this is also important, as it indicates that no one individual stress dominates the thermal abilities of *I. purpureus* workers on site.

Critical thermal maxima of individual ants ranged between 41.5°C and 56.1°C, and CT_{min} between 0.3°C and 7.1°C in this study. This is a very wide range of readings for CT_{max}, and could be due to age, nutritional status, stress or prior heat exposure that the ants may have been exposed to (Nyamukondiwa & Terblanche 2009; Sørensen et al. 2001). Upper thermal limits are thought to be less plastic compared to lower limits, however it is known that environmental exposure does influence these limits (Hoffmann et al. 2013), and this is seen with the relationships with both LUI and Clay in this study. Here we measured CT_{max} and CT_{min} by observing an individual ant's ability to right itself while temperatures were increasing at 0.25°C min^{-1}. The calculation of critical thermal limits using ant righting behaviour may be more variable than using physiological critical limits such as upper lethal temperatures where ants are exposed to static temperatures for two hours (Andrew et al. 2013a) or thermolimit respirometry where CT_{max} is derived from metabolic measurements using flow-through CO_2-based respirometry and optical detection, when temperatures are ramped at a consistent rate (Andrew et al. 2016; Lighton & Turner 2004). As an alternative measure of CT_{max} thermolimit respirometry (Lighton & Turner 2004) may be more robust, as the method explicitly measures the ceasing of metabolism (release of carbon dioxide) of the ant; but it is also a different measure of CT_{max}, as there is no ability for the ants to recover from heat exposure in thermolimit respirometry.

When the fitted models were used to assess critical thermal limits, it is clear that site specific differences strongly influenced the results found. However, land use and soil clay content also played a significant role in influencing ant physiological end-points. This suggests that ant populations that were exposed to higher levels of habitat modification (via land use intensity) showed lower climatic resilience relative to less disturbed habitats. However, there is still additional unaccounted for variation in the residuals which suggests that there may be other variables (unmeasured) that may have an effect on the meat ants' climatic resilience.

For ants, much of the research on local effects of habitat disturbance has been carried out on changes in communities (Andersen & Majer 2004; Andrew et al. 2000; Bromham et al. 1999). Previous work carried out along the gradient (Oliver et al. 2016) used for this study found clear evidence for landscape adaptation to maintain and restore species richness of ant communities at the site level. For ant communities, higher woody native cover and shrub cover, and lower exotic plant groundcover have a positive effect on ant species richness. Interestingly, Land Use Intensity had no significant impact on the species richness within any of the ant genera assessed across the gradient.

However, clay did have a positive influence on *Iridomyrmex* spp. diversity in Oliver et al. (2016). Clay and clay-like substrate is an important component for ant nest development (Monaenkova et al. 2015), and is critical for other insect taxa, such as termites in giving their feeding galleries structural support to assist with load bearing (Oberst et al. 2016). As *I. purpureus* nests are known to be located in the same location for over 70 + years (Greenslade 1975), substantive structural elements are required to keep it maintained during this time. The amount of clay in a *I. purpureus* nest is representative of the surrounding non-nest soil (Ettershank 1968). *Iridomyrmex purpureus* nests are also not found on quartz sand soils, even when climatic factors are suitable, indicating that soil type can be a limiting distributional factor (Greaves 1971). As clay plays a role in the distribution of the species, it also clearly pays a role in the physiological breadth of individuals.

For the CT_{max} model fitting, there was one model with a lower AIC (in which the interaction between LUI*Canopy) was included. This was a more complex model, and so was not deemed the most appropriate to best explain the CT_{max} relationship. In addition, the current model is simpler to interpret and also in line with the results for CT_{min}.

We calculated warming tolerance using three different measures of habitat temperature, all generated based on location data using ANUCLIM. These all indicated, as expected, that an increase in aridity reduces ant tolerance to warming. When the warming tolerance was previously calculated for *I. purpureus* at a higher altitude (Armidale, NSW: 980 masl), similar calculations were made: a warming tolerance of 19.5°C was calculated on weather station summer average, and 25.8°C based on weather station annual average (Andrew et al. 2013a). As Armidale is a more temperate site than those tested here, it would be at the lower scale of the aridity index. Across the aridity index there is a 10°C difference in warming tolerance for *I. purpureus*. With a prediction of global increases in air temperature of 2°C and 6°C over the 21st Century, and in the region assessed there is an 80% probability of a 3°C warming and a 30% probability of a 4°C warming with a likelihood of reduced annual rainfall of 3-5% (CSIRO-ABM 2012), aridity of the region assessed will only continue to increase.

Conclusion

From this study we have found that habitat type (e.g. soils) and land-use intensity are more limiting factors on meat ant CT_{max} and CT_{min} than climatic factors (here we tested aridity). These populations are key ecosystem engineers and as they are put under more stress, wider ecological implications may occur if population abundances decline, as we expect to see a reduction in the physiological resilience of *I. purpureus* as land use intensity increases.

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Table 1(on next page)

Characteristics of the 11 sites used in this study (from a total of 87). See Oliver *et al.* (2016) for details on the full complement of sites.

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Table 1. Characteristics of the 11 sites used in this study (from a total of 87). See Oliver *et al.* (2016) for details on the full complement of sites.

Site name	**Aridity**	**Altitude**	**Land Use Intensity**	**Soil Clay**	**Total native woody cover**	**Exotic Ground Cover**	**pH**	**Lat**	**Long**
Smokey Mountain (38)	0.401	891	2	5	23	50	4.585	-29.966	151.271
Furrocabad Station (44	0.346	1047	3	28.8	30	69	5.25	-29.83	151.608
Furrocabad Station (45)	0.366	1008	8	28.8	97	68	5.64	-29.823	151.598
Delunga 52	0.617	338	0	37.5	76	9	6.16	-29.835	150.554
62	0.716	203	4	27.5	16	43	5.675	-29.379	149.797
63	0.715	204	5	30	66	2	5.855	-29.378	149.796
87C	0.732	163	6	57.5	1	83	6.425	-29.693	149.23
Towarra (96)	0.537	643	1	28.8	70	1	5.56	-30.125	150.76
Myall Creek (117)	0.583	457	1	65	68	18	6.465	-29.823	150.74
West Oaks (126C)	0.491	730	4	15	97	2	5.89	-29.359	151.429
West Oaks (127C)	0.508	683	5	53.8	1	10	5.695	-29.36	151.412

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Table 2(on next page)

Estimated fixed effects for the selected CT$_{max}$ model. Standard errors and 95% confidence intervals are also presented. All variables have been centred.

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Table 2. Estimated fixed effects for the selected CT_{max} model. Standard errors and 95% confidence intervals are also presented. All variables have been centred.

	Estimate	Std. Error	2.5 %	97.5 %
(Intercept)	46.04	0.30	45.52	46.54
Land Use Intensity (LUI)	-0.28	0.15	-0.48	-0.06
Total native woody cover (Canopy)	0.01	0.01	-0.014	0.02
Exotic groundcover	0.01	0.01	-0.01	0.03
Soil Clay Content	0.04	0.02	0.01	0.06
Aridity Index	2.82	2.54	-6.37	0.18

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Table 3(on next page)

Estimated fixed effects for the selected CT_{min} model. Standard errors and 95% confidence intervals are also presented. All variables have been centred.

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Table 3. Estimated fixed effects for the selected CT_{min} model. Standard errors and 95% confidence intervals are also presented. All variables have been centred.

	Estimate	Std. Error	2.5%	97.5%
(Intercept)	3.7	0.37	2.85	4.28
Land Use Intensity	-0.091	0.18	-0.34	0.15
Total native woody cover (Canopy)	0.00	0.013	-0.03	0.02
Exotic Groundcover	0.004	0.016	-0.02	0.023
Soil Clay Content	0.017	0.025	-0.01	0.06
Aridity Index	0.29	3.3	-4.24	5.01

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Figure 1(on next page)

Sites used in this study in northern New South Wales, Australia (see insert) with relative values for CT_{max} (A), Land Use Intensity (B), Aridity (C), and Clay (D) shown.

Maps generated using Map data © OpenStreetMap contributors. The size of the circle is indicative of the mean value of the given variable (i.e. the larger the circle, the higher the value, and the contrary). Image produced using the Leaflet package (version 1.1.0.9000, http://rstudio.github.io/leaflet/) within R statistical software (version 3.4.3). The R package OpenStreetMap is licensed under a GNU General Public License (GPL-2) (https://cran.r-project.org/web/packages/OpenStreetMap/index.html) and was used to extract map tiles from OpenStreetMap which is licensed on terms of the Open Database License, “ODbL” 1.0. (http://wiki.osmfoundation.org/wiki/Licence).

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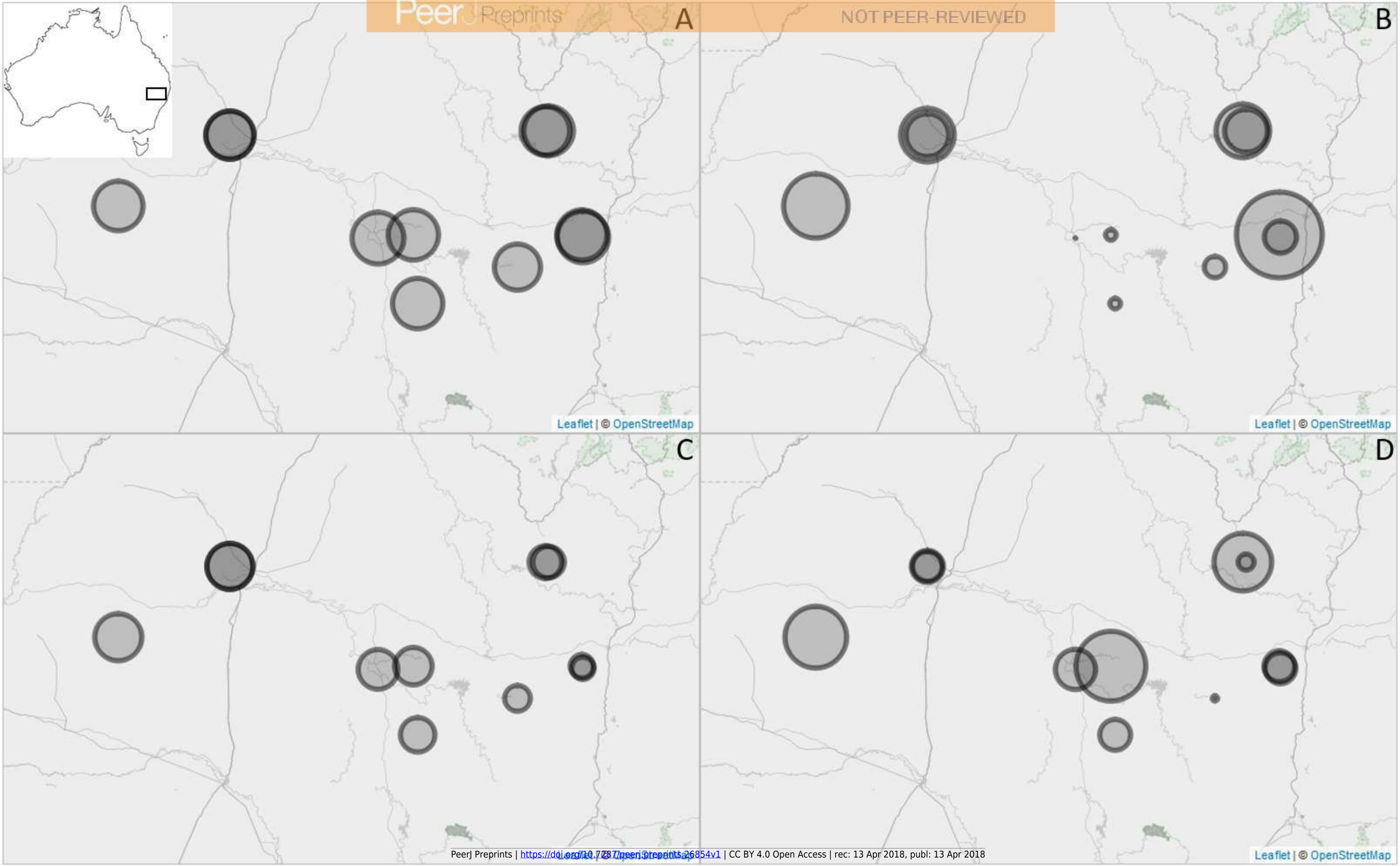

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Figure 2(on next page)

Random effect estimates of model coefficients using Best Linear Unbiased Prediction (BLUP) and 95% confidence intervals of the intercepts and CT_{max} (centred – Ctmaxc) and CT_{min} (centred – Ctminc) across sites.

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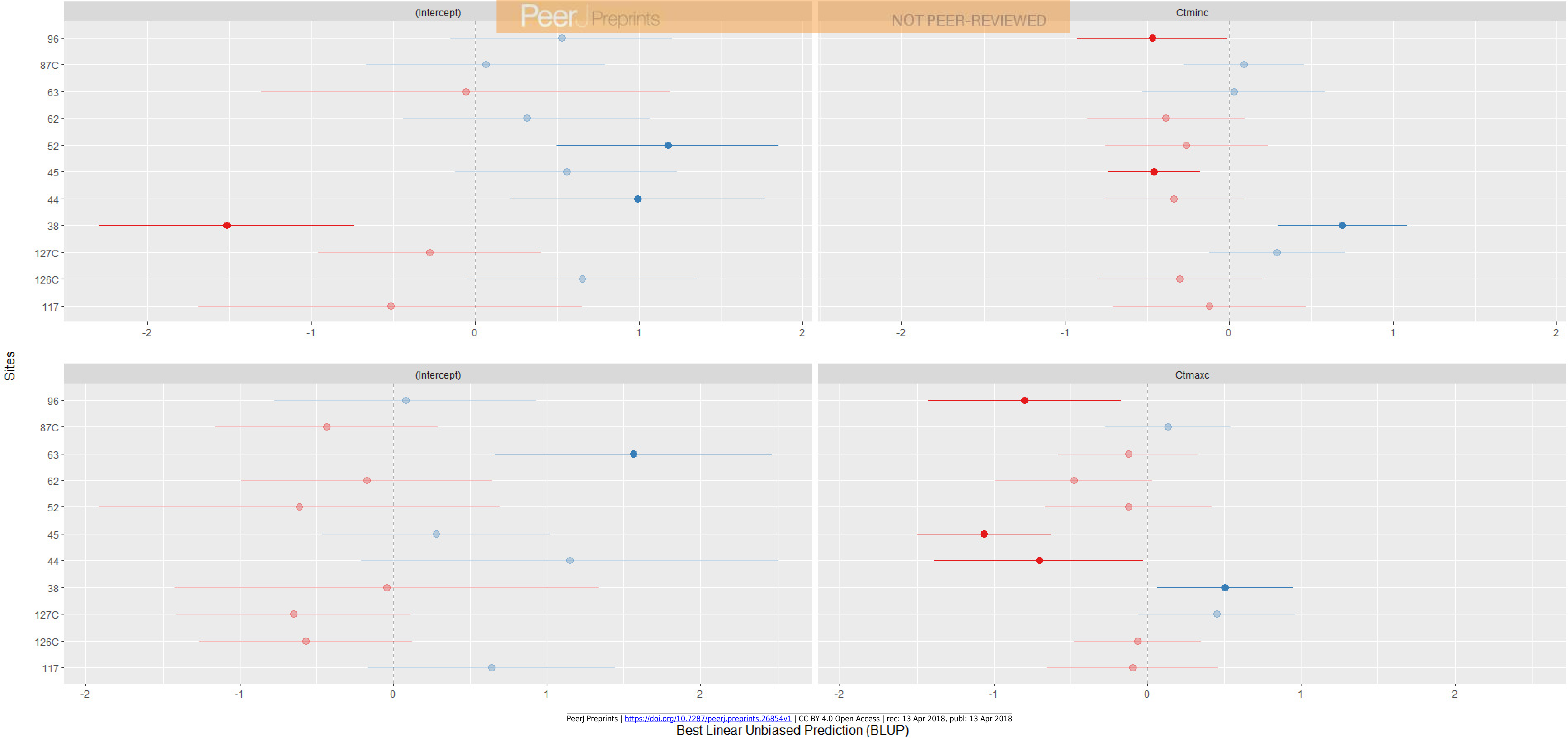

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Figure 3(on next page)

95% confidence intervals on the selected CT_{max} and CT_{min} models for the standardised factors of Land Use Intensity (LUI) and Clay.

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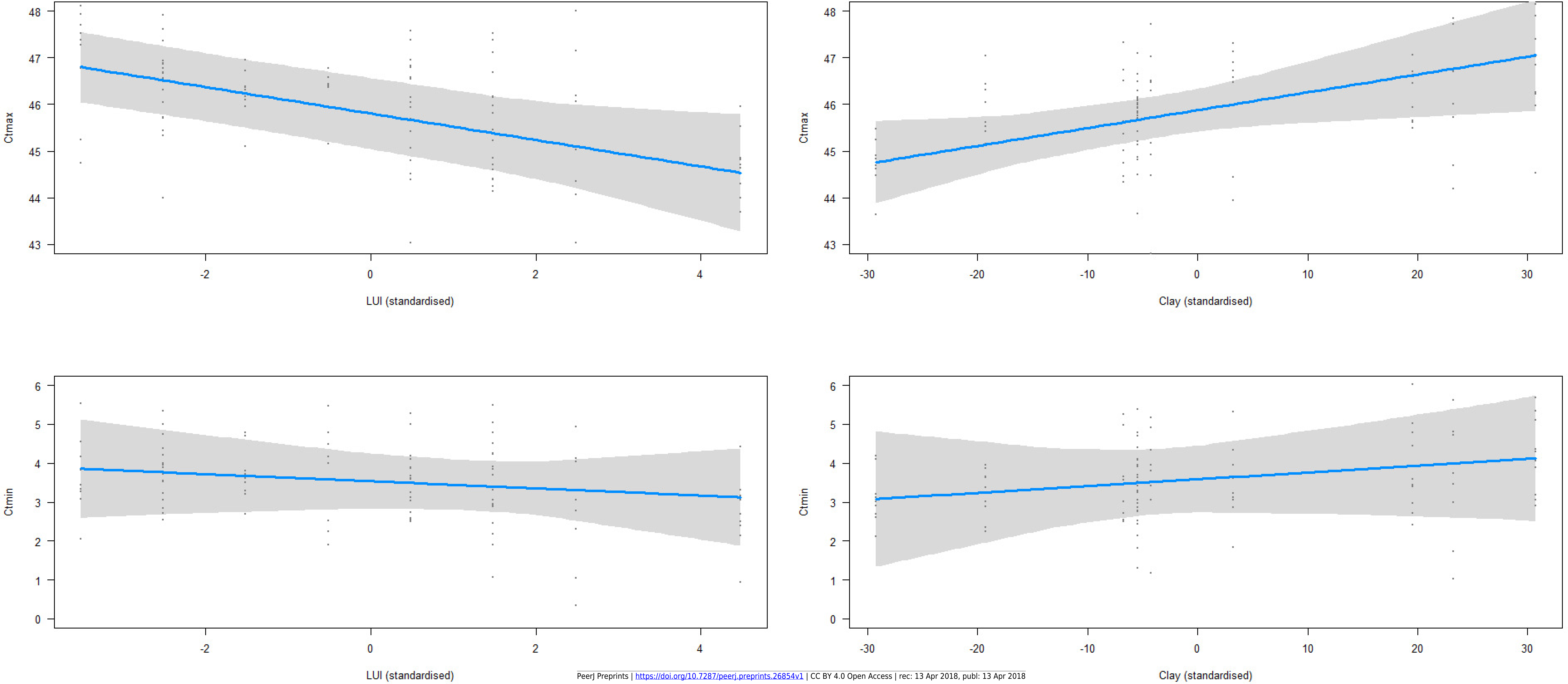

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Figure 4(on next page)

Three measures of warming tolerance (3 months, 12 months and 36 months); based on location modelled ANUCLIM data for three different sampling periods) relative to aridity index for each site.

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