

Urbanisation dampens the latitude-diversity cline in ants

Abe Perez^{1,2}  | Lacy Chick^{1,3} | Sean Menke⁴ | Jean-Philippe Lessard⁵  | Nathan Sanders⁶ | Israel Del Toro⁷ | Niklas Sundebo Meldgaard⁸ | Sarah Diamond¹

¹Department of Biology, Case Western Reserve University, Cleveland, Ohio, USA

²Center for Clinical Research, University Hospitals, Cleveland, Ohio, USA

³Hawken School, Gates Mills, Ohio, USA

⁴Department of Biology, Lake Forest College, Lake Forest, Illinois, USA

⁵Department of Biology, Concordia University, Montreal, Quebec, Canada

⁶Department of Ecology and Evolutionary Biology, University of Michigan, Ann Arbor, Michigan, USA

⁷Biology Department, Lawrence University, Appleton, Wisconsin, USA

⁸Skolen i Bymidten, Helsingør, Denmark

Correspondence

Abe Perez, Department of Biology, Case Western Reserve University, Cleveland, Ohio, USA.

Email: jap194@case.edu

Editor: Yves Basset and Associate Editor: Jerome Orivel

Abstract

1. The increase in species diversity from temperate to tropical regions is one of the most widespread patterns in biogeography. As humans continue to drastically modify natural habitats, land-use changes such as the development of cities could potentially alter typical latitudinal diversity gradients. Cities could depress or enhance biodiversity through filtering, localised extirpations, or increasing niche availability, respectively.
2. To address these possibilities and the consequences for the latitudinal diversity gradient, we constructed a global dataset of urban species diversity (richness) and community composition across $\sim 60^\circ$ of absolute latitude and from 63 cities. We focused our study on ants, for which comparable urban and non-urban diversity data are broadly available.
3. We found that urbanisation significantly dampened the latitude-diversity cline. The effects of urbanisation varied with latitude: at lower latitudes, cities were relatively species poor and harboured distinct ant communities relative to nearby non-urban communities. In higher latitude cities, both species richness and community composition were more similar to the surrounding non-urban ant communities.
4. Our analyses suggest that the strongest impacts of urbanisation on ant diversity may be in the tropics, where biological diversity is already expected to experience the greatest risk of extinction in the face of climate change.

KEYWORDS

community composition, latitude-diversity, macroecology, species richness, urbanisation

INTRODUCTION

One of the most frequently documented patterns in macroecology is the latitudinal diversity gradient, where species diversity decreases with increasing latitude (Gaston, 2000; Hillebrand, 2004; Willig et al., 2003). With the emergence of global datasets, multiple studies have investigated why this relationship exists and have developed multiple hypotheses explaining this pattern, including species–energy relationships, and systematic differences in speciation and extinction rates (Gaston, 2000; Hillebrand, 2004; Willig et al., 2003). These advances have improved our understanding of the patterns and drivers of global biodiversity. However, few studies have considered

how human alterations to natural environments, such as urbanisation, might modify or disrupt these well-established relationships. This is despite the recognition of the potential impact of urbanisation on local-scale patterns of biodiversity (Baldock et al., 2015; Nilon, 2011; Sadler et al., 2010).

With over half of the world's population now living in cities (United Nations Department of Economic and Social Affairs, 2015) and approximately 3% of the global terrestrial surface consisting of heavily altered urban land cover (Liu et al., 2014), urbanisation represents a pervasive anthropogenic challenge for biodiversity. At a global scale, the processes associated with urbanisation typically reduce species richness relative to the surrounding natural areas

(Aronson et al., 2014; Grimm, Faeth, et al., 2008; Grimm, Foster, et al., 2008; Luck & Smallbone, 2010; Niemelä & Kotze, 2009; Saari et al., 2016; Wenzel et al., 2020). These losses are exacerbated by human-mediated introductions of exotic species, which often generate novel, but species-poor communities through the replacement and suppression of native species (Gippet et al., 2017; McGlynn, 1999; Sanders et al., 2003; Winter et al., 2009). Moreover, the addition of exotic species is often insufficient to recoup the loss of native species diversity in cities (Faeth et al., 2011). Coupled together, biological communities in cities often have fewer species, and/or different species, from those of the surrounding natural communities. Such urban-

specific loss of native species might therefore decrease the typical latitude–diversity relationship in cities if few exotic species replace many native species (Figure 1a). Alternatively, cities might cause the typical latitude–diversity relationship to become noisier rather than systematically dampened (Figure 1b). Recent studies have challenged the universality of urban biodiversity loss by demonstrating that diversity in some cities is maintained or even increases relative to surrounding non-urban areas (Hill et al., 2017; Menke et al., 2011; Perez & Diamond, 2019; Saari et al., 2016). If cities harbour idiosyncratic gains and losses of biodiversity, the latitude–diversity relationship might therefore simply become noisier, depending on the magnitude of the urban–non-urban diversity change relative to the latitudinal signal.

Another important consideration for the impact of urbanisation on the latitude–diversity relationship is whether the effects of urbanisation on biodiversity themselves systematically vary with latitude (Figure 1c). For example, a latitudinal cline in the effects of cities on biodiversity could be driven by shifts in the costs and benefits of urban warming across latitude. Urban heat island effects are a consistent feature of cities across latitude (Oke, 1982); however, urban heat islands could be expected to have benign consequences on biodiversity at higher latitudes, but detrimental consequences at lower latitudes. As ectothermic species tend to be thermally limited by cold temperatures at high latitudes, cities could relax this constraint where background temperatures are cooler. In contrast, ectothermic species tend to be near their limits of thermal performance at low latitude, in which case, cities could induce thermal stress in these warmer background temperature environments (Deutsch et al., 2008; Ghalambor et al., 2006; Tewksbury et al., 2008). Thus, rates of species loss in cities could be disproportionately high in the tropics. Although data are currently sparse, some studies are suggestive of urban diversity preservation at higher latitudes and loss at lower latitudes (Youngsteadt et al., 2017). Such a pattern could create a dampening effect on the

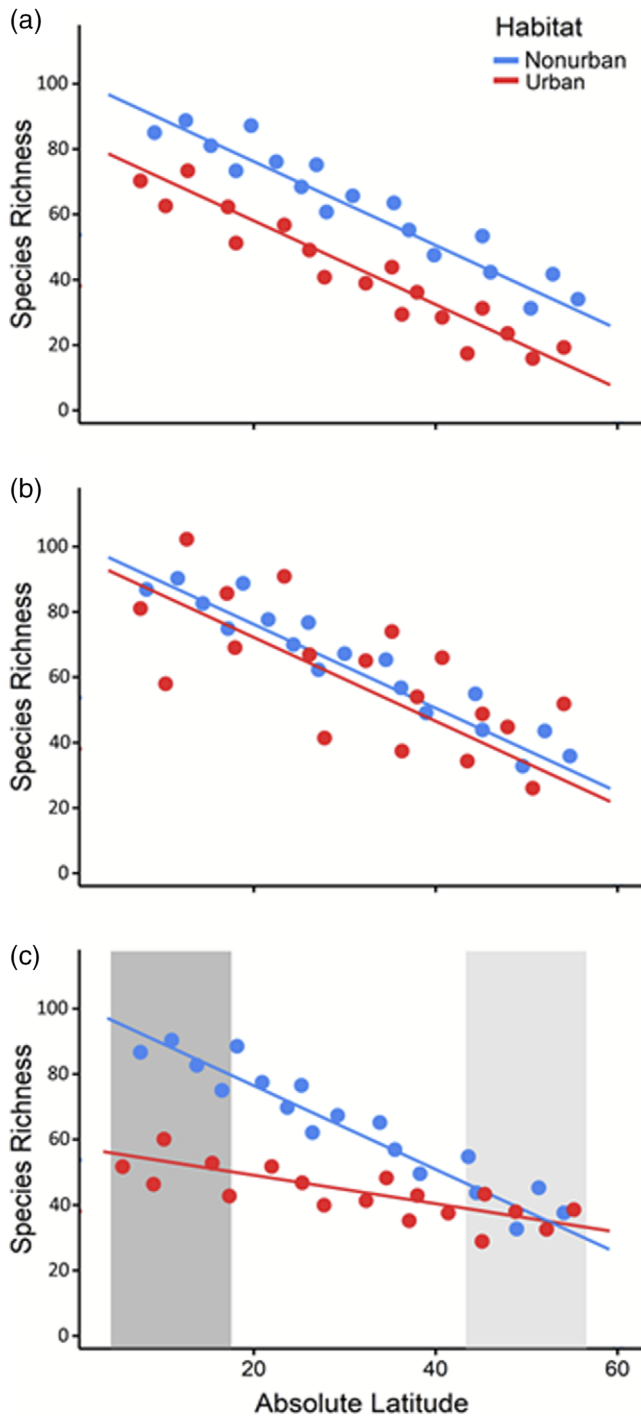


FIGURE 1 Three alternative hypotheses for the impacts of urbanisation on the latitude–diversity cline, including (a) urban-specific loss of species diversity, (b) idiosyncratic gains and losses, and (c) differential urban impacts across latitude. (a) Consistent losses in urban species richness (red points), resulting in biological communities that are species poor relative to non-urban species richness (blue points). (b) Cities may harbour idiosyncratic gains and losses of biodiversity. Under this scenario, the broader latitude–diversity cline is maintained across cities, although noisier relative to non-urban species richness change. (c) The impact of urbanisation on the latitude–diversity cline may vary with latitude. In this example, species richness loss may be disproportionately high at lower latitude cities (within dark grey box) and less so at higher latitude cities (within light grey box). Several additional alternative hypotheses are not shown: one in which cities uniformly increase diversity; one in which urban diversity is enhanced only at low latitudes; and one in which urban diversity is enhanced only at high latitudes. This is because our main hypotheses are derived from theory and empirical support, and these other alternative hypotheses are currently unsupported (though nonetheless possible), including specifically in ant systems (Gibb et al., 2015).

latitude-diversity cline, with the effects of urbanisation varying with latitude (Figure 1c).

We compiled a dataset of species richness and community composition of ants in cities and adjacent non-urban areas to examine the impacts of urbanisation on the latitude-diversity gradient. We focused on ants, as they are ubiquitous in nearly every terrestrial ecosystem, including cities, and patterns of global ant diversity closely follow patterns of other taxa (Dunn et al., 2010; Economo et al., 2018; Kaspari et al., 2003; Kusnezov, 1957; Lach et al., 2010; Moreau & Bell, 2013; Santos, 2016). Furthermore, ants already exhibit a strong latitude-diversity relationship, making them an excellent candidate system to explore the impacts of urbanisation on latitudinal clines in diversity (Kusnezov, 1957). Finally, ant diversity is highly responsive to biogeographic variation in climate including temperature and precipitation, as well as to variation in habitat disturbance (Gibb et al., 2015). Using a paired study design wherein we calculated the species richness of individual cities and nearby non-urban communities, we tested whether cities dampened the latitude-diversity gradient, that is, whether ant species richness in cities was reduced relative to that in surrounding areas. We then explored the basis for our observed patterns, specifically by asking: (1) whether urbanisation tends to reduce diversity, (2) whether urban community composition differs from the nearby non-urban community, and (3) whether impacts of urbanisation on diversity and composition vary across latitude.

MATERIALS AND METHODS

Developing the ant species richness and community composition database

We developed a global ant species richness dataset derived from studies conducted in both urban and non-urban areas (hereafter

referred to as habitat). To develop the urban data subset, we consolidated georeferenced data of species richness and community composition by searching Google Scholar and Web of Science using the following keywords: urban, ants, community, richness, and diversity (last accessed date: 6 November 2019). From this search, we found 35 studies (63 cities) that reported species richness in urbanised environments (Figure 2; Table S1). We defined urban environments as sites located within city boundaries, outdoors and embedded within urban development; no samples from within buildings were included. These studies followed standard ant survey protocols such as pitfall trapping, timed hand sampling, baiting, and litter extractions (Bestelmeyer, 2000). Due to the limited number of studies investigating ant species richness in cities, our analyses used raw values of species richness as opposed to rarified values. Sampling method and effort varied among studies, and few studies reported a measure of species abundance. As a result, we were unable to effectively subset the data by sampling method or reported metrics; however, this potential confounding effect was controlled for in our analyses by including study ID as a model term (Pautasso et al., 2011).

Next, we gathered non-urban ant species richness data, using the Global Ants Database (GLAD, Gibb et al., 2017). We selected non-urban studies by identifying georeferenced GLAD records within the region of each city (250 km radius buffer around each city with urban species richness data). Owing to the large amount of interspecific variation in flight dispersal distances (four orders of magnitude Helms, 2017), we selected this radius as it would reasonably separate regional scale species pools, that is, the radius is over 30 times the mean of known ant flight distances (Helms, 2017). We found 50 studies (57 sites) that met this criterion (Figure 2; Table S1).

Lastly, we used a combined dataset across the 35 urban and 50 non-urban studies to explore differences in community composition. To develop the urban data subset, we identified urban studies

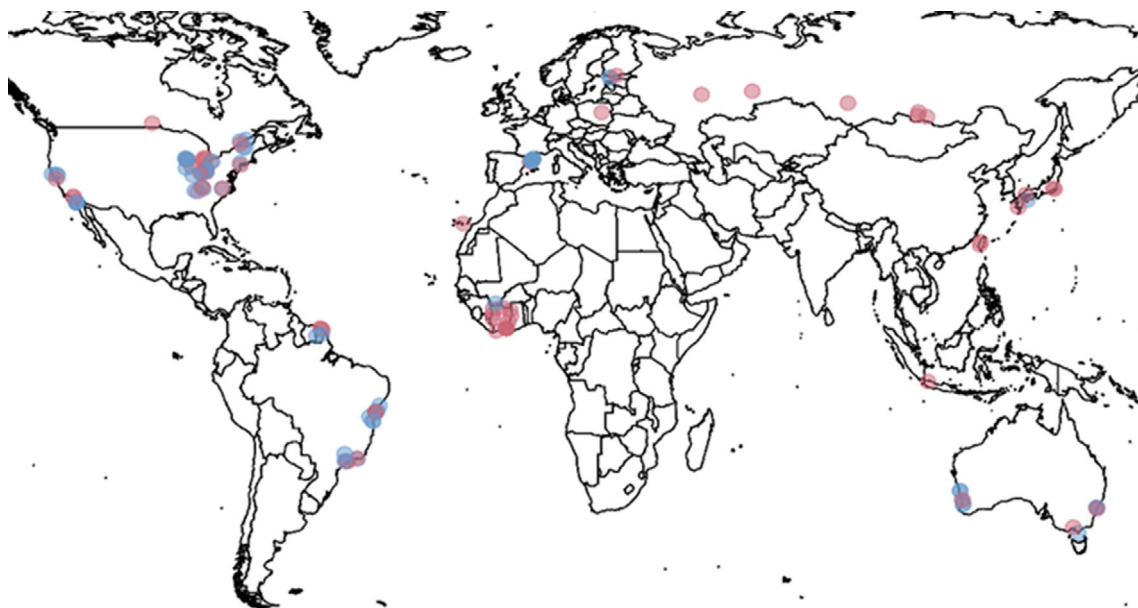


FIGURE 2 Geographic location of study sites used in analyses. Red points represent urban sites and blue points represent non-urban sites.

that minimally identified morphospecies within genera, sampled within a focal city. To develop the non-urban data subset, we identified regional non-urban studies (within a 250 km radius around each city) that similarly reported at least morphospecies within genera. This resulted in 30 pairs of urban and non-urban (morpho-)species lists, each pair matched by city.

Controlling for intercity variation in the degree of urbanisation

As the degree of urbanisation could potentially influence absolute differences in ant species richness among cities and relative differences in community composition between urban and non-urban paired sites, we quantified the degree of urbanisation for the region of each city in our study. We estimated the mean percent-developed impervious surface area (ISA) of a 250 km buffer, using data derived from the global density of constructed ISA data set (Elvidge et al., 2007). ISA is the percentage of surface area covered by artificial surfaces such as concrete, with larger percentages indicating increased urban development. Mean ISA was calculated using the *zonal statistics* tool in ArcGIS v10.4.

Statistical analyses

The effect of urbanisation on the latitude-diversity cline

To examine the impacts of urbanisation on the latitude-diversity cline in ants, we constructed a series of linear mixed-effects models with the main effects and interaction effects of habitat (urban and non-urban) and latitude (absolute latitude). In some cases, multiple reports of species richness originated from the same study (54/120 observations, 15/81 studies); therefore, we modelled 'study ID' as a random effect to account for the non-independence of values from the same study. This model allowed us to evaluate several hypotheses and predictions: (1) urban dampening of the latitude-diversity cline would be indicated by a significant habitat \times absolute latitude interaction term with the slope for the urban habitat being smaller than the non-urban habitat; this outcome agrees with our a priori prediction; (2) conversely, a significant habitat \times absolute latitude interaction term with the slope for the urban habitat being greater than the non-urban habitat would indicate urban enhancement of the latitude-diversity cline; this outcome is against our a priori prediction, but plausible if cities have marginal reductions in biodiversity at low latitudes and more substantial species losses at high latitudes; (3) a non-significant habitat \times absolute latitude interaction term would indicate similar latitude-diversity clines across urban and non-urban habitats, assuming the latitude main effect is still significant to demonstrate the presence of the already well-established latitude-diversity cline in ants from unaltered habitats; although this outcome is against our a priori prediction, it is nonetheless plausible if cities only have marginal impacts on biodiversity; and (4) a non-significant habitat \times absolute latitude interaction term but with significant main effects of absolute

latitude and habitat type, particularly in which the urban mean biodiversity is lower than non-urban, would indicate that cities reduce biodiversity, but do so similarly across latitude, that is, that cities proportionally reduce biodiversity relative to the non-urban species pool; this outcome is against our a priori prediction, but plausible if latitude is the primary filter on diversity, with city effects on diversity acting secondarily and in proportion to regional species pool diversity.

In the event of a significant interaction between habitat and absolute latitude, we further used this as justification to quantify the latitudinal cline for each habitat type separately. To accomplish this, we performed separate linear mixed-effect models for each habitat type, urban and non-urban. Finally, we quantified the degree to which the urbanisation effect alters estimates of the latitude-diversity relationship, by constructing a linear mixed-effect model pooled across habitat type, with the main effects of absolute latitude, and the random effect of 'study ID'. We then compared model coefficients from the habitat-pooled model to the separate non-urban only model. All analyses of species richness were performed using the *nlme* package (Pinheiro et al., 2017) in R (R Core Team, 2018).

The effect of urbanisation on community composition

After exploring the effects of urbanisation on the latitude-diversity cline, we explored changes in community composition. We used permutational multivariate analysis of variance (PERMANOVA) based on genus occurrence and using Sørensen (which is appropriate for occurrence-based data) dissimilarity matrices. Species-level data were not available for all studies included in the analysis; however, genus and species diversity have been found to be highly correlated when describing biodiversity patterns in ants. We included habitat type (urban and non-urban), absolute latitude and their interaction as predictors. We performed 999 permutations for each test (McCordle & Anderson, 2001). With this analysis, we were able to specifically ask whether cities harboured unique ant communities or whether they had similar community composition as nearby non-urban areas (as assessed with the significance of the habitat type term), and whether these trends depended on latitude (as indicated by a statistically significant interaction between habitat type and absolute latitude). To visualise shifts in community composition, we performed non-metric multi-dimensional scaling (NMDS) based on a genus occurrence, Sørensen dissimilarity matrix ordinated along two dimensions. Both analyses for community composition were conducted with the *vegan* package (Oksanen et al., 2017).

RESULTS

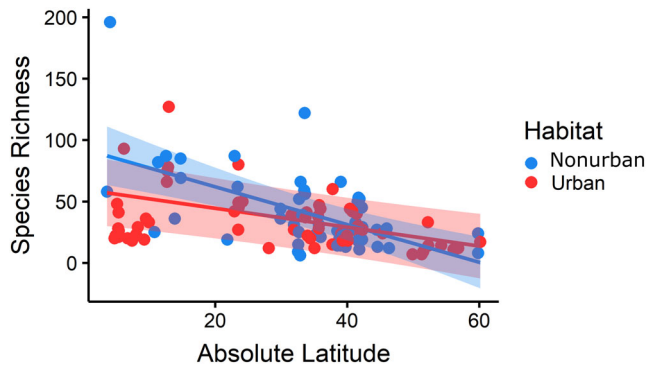
Urbanisation dampens the latitude-diversity cline in ants

The number of ant species in non-urban communities declined as latitude increased (Table 1, Figure 3). However, and consistent with our

TABLE 1 Estimates and statistical significance of the predictors habitat (urban vs. non-urban), absolute latitude and their interaction on ant species richness from a linear mixed-effects model

Term	Estimate	SE	χ^2	<i>p</i>
Habitat	-41.363	14.357	23.632	<0.0001
Absolute latitude	-1.624	0.284	33.033	0.003
Habitat × absolute latitude	1.008	0.388	17.816	0.008

Note: Estimates show differences from non-urban habitats. Significance was assessed using likelihood ratio tests. Significant *p* values are in bold.

**FIGURE 3** Relationship between species richness and absolute latitude, between urban (red points) and non-urban (blue points) habitats, with predicted values (solid lines) and 95% confidence intervals (ribbons)**TABLE 2** Estimates and statistical significance of separate linear mixed-effects models, examining the predictor of absolute latitude on ant species richness

Model	Estimate	SE	χ^2	<i>p</i>
Urban only	-0.769	0.212	13.543	<0.001
Non-urban only	-1.537	0.330	22.509	<0.0001
Habitat-pooled	-1.126	0.211	29.028	<0.0001

Note: Models include urban only (species richness values subsetted to those that originated from cities), non-urban only (species richness values subsetted to those that originated from natural sites), and habitat-pooled (both urban and non-urban species richness values are included; model does not differentiate by habitat type). Significance was assessed using likelihood ratio tests. Significant *p* values are in bold.

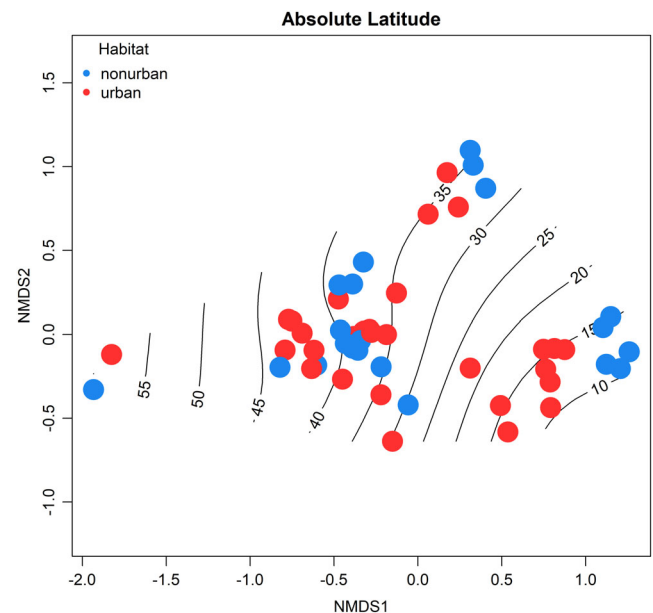
TABLE 3 PERMANOVA summary table examining differences in ant communities across habitat (urban and non-urban), absolute latitude, and their interaction

Term	<i>F</i>	<i>R</i> ²	<i>p</i>
Habitat	2.792	0.028	0.033
Absolute latitude	35.890	0.363	0.001
Habitat × absolute latitude	4.078	0.041	0.004

Note: Significant *p* values are in bold.

Abbreviation: PERMANOVA, permutational multivariate analysis of variance.

expectation (Figure 1c), urbanisation dampened, but did not eliminate, the latitude-diversity cline. Indeed, we found a significant interaction between habitat and absolute latitude ($p = <0.001$; Table 1, Figure 3)

**FIGURE 4** Nonmetric multidimensional scaling (NMDS) ordination of genus-level community composition. Each point represents the genus composition of each habitat (urban = within city, non-urban = within 250 km buffer around a city). Labelled contour lines denote latitudinal trends.

such that the decline in diversity with increasing latitude was more steep for the non-urban habitat communities compared with the urban habitat communities (non-urban: $\beta = -1.537$, $\chi^2 = 22.509$, $p = <0.0001$; urban: $\beta = -0.769$, $\chi^2 = 13.543$, $p = <0.001$; Table 2, Figure 3). The difference in the latitudinal diversity gradient between cities and non-urban areas changed slightly when we accounted for variation among cities in their degree of urbanisation (approximated by ISA). When we compared the slope estimate from the habitat-pooled model of species richness (pooled across habitat type) to that of the model with only the non-urban data, we found a difference of nearly 0.5 (habitat-pooled model: $\beta = -1.126$, $\chi^2 = 29.028$, $p = <0.0001$; non-urban only model: $\beta = -1.537$, $\chi^2 = 22.509$, $p = <0.0001$; Table 2). In other words, for every 1-degree change in absolute latitude, diversity was being underestimated by half a species in the model that ignored the effect of urbanisation.

For both the species richness and community composition analyses described below, the inclusion of the magnitude of urbanisation (ISA) of a given city did not qualitatively change our results (Tables S2

and S3). To simplify our analyses, we excluded ISA from the final models.

Community composition in urban and non-urban ant communities is similar at high latitudes, but not low latitudes

Ant community composition differed between urban and non-urban habitats, varied with absolute latitude, and depended on the interaction between habitat and latitude (Table 3), suggesting that differences between urban and non-urban composition varied geographically (Figure 4, stress = 0.1080). Specifically, at high latitudes, urban and non-urban communities were similar in composition, but tended to diverge at low latitudes to the extent that in the tropics, urban communities were unique groups of species rather than subsets of the non-urban regional species pool.

DISCUSSION

The latitudinal-diversity gradient is one of the most widely observed, fundamental patterns in ecology (Gaston, 2000; Hillebrand, 2004; Willig et al., 2003). While this relationship has long been a central aspect of ecological research (Hawkins, 2001), there is still a lack of consensus on the underlying mechanisms (Economio et al., 2018; Gaston, 2000; Wang et al., 2011, 2009) and even less of an understanding on how malleable this pattern may be, particularly when considering ongoing global anthropogenic change, such as invasion and urbanisation (Arnan et al., 2017). Cities can radically change the landscape and local climate (Grimm, Faeth, et al., 2008; Grimm, Foster, et al., 2008). However, few studies to date have examined whether urbanisation may alter latitudinal diversity gradients. Here, we found that urbanisation dampens the latitudinal diversity gradient for ants (Figure 3), largely driven by differential urban effects across latitude, where cities at lower latitudes are relatively species poor and harbour unique collections of species that are distinct from the nearby non-urban species pool (Figure 4). In contrast, at higher latitudes, there was no difference in species richness nor composition between urban and non-urban sites. As a result, the strongest and most detrimental consequences on biodiversity were observed in cities at lower latitudes, a species group already at greatest risk of extinction in the face of ongoing climate change (Deutsch et al., 2008; Huey et al., 2009; Tewksbury et al., 2008).

Consistent with previous findings of ant species diversity change along broad latitudinal gradients (Dunn et al., 2010; Economio et al., 2018; Kaspari et al., 2003; Kusnezov, 1957; Ward, 2010), non-urban ant species richness was greatest at the lowest latitudes, and decreased at higher latitudes. However, while the same overall pattern held true for urban ant species richness, the degree of change was far less, with urban ants exhibiting a relatively flatter diversity-latitude cline compared with that of non-urban ants. These results were further supported by our comparisons of our habitat-pooled

model of species richness to the non-urban only model. Our habitat-pooled model estimated a decrease of approximately 1 species per 1-degree change in latitude, where the non-urban only model found that when only considering values originating from 'natural' sites, species richness should decrease approximately 1.5 species per 1-degree increase in latitude. In other words, by ignoring the source of the species richness values, our model misestimated latitudinal species richness change by approximately 0.5 units. While this discrepancy is seemingly small, considering the compounding effect across the latitudinal range presented in this study (approximately 0°–60° of absolute latitude), urbanisation may result in severely reduced biodiversity estimates across geographic space. From a practical standpoint, these results indicate that studies ignoring the source of species richness can have profound effects on estimates of global species richness change. Additionally, studies exploring natural biodiversity should be cautious of the proximity of study sites to nearby urban development. The physical footprint of cities is increasing globally, in order to accommodate a growing urban population (Liu et al., 2014; Seto et al., 2012), and as such, cities are no longer compact, and instead sprawl out, developing peri-urban and suburban areas (Batty, 2008). As a result, the ecological impacts of urbanisation may extend beyond city boundaries, influencing biodiversity at regional scales, or as we found here, at global scales as well.

Interestingly, we found that the urban latitude-diversity cline was still present, if dampened. Specifically, because we did not find an invariant relationship between urban diversity and latitude, our study suggests that there is no fixed carrying capacity in cities as would be necessary to completely erase the latitude-diversity cline in ants. Our analyses of species richness and community composition lend support to both negligible or incomplete replacement of urban diversity at high latitude and higher rates of species loss in the tropics as explanations for the present, but dampened latitude-diversity cline. Indeed, our study might help to reconcile contrasting results for the impacts of urbanisation on diversity: at lower latitudes, our study is consistent with research showing that biological communities within cities are often species poor and highly dissimilar to the surrounding non-urban communities (Aronson et al., 2014; Grimm, Faeth, et al., 2008; Grimm, Foster, et al., 2008; Luck & Smallbone, 2010; Winter et al., 2009). The magnitude of the tropical urban biodiversity loss was appreciable in our dataset: over 100 species were lost from our lowest latitude city as compared with nearby non-urban sites. In contrast, at higher latitudes, our study is consistent with studies showing that cities can maintain or increase diversity, even among native species (Perez & Diamond, 2019; Saari et al., 2016), possibly through greater availability of limiting resources, or buffered seasonal fluctuations (Faeth et al., 2011).

When investigating shifts in community composition, we found significant effects of habitat type and latitude. While shifts in community composition, in response to urbanisation, have been documented by numerous studies (Clergeau et al., 2006; Grimm, Faeth, et al., 2008; Grimm, Foster, et al., 2008; Hodges & McKinney, 2018; Knop, 2016; Kühn & Klotz, 2006; Thompson & McLachlan, 2007; Van Nuland & Whitlow, 2014) our results suggest that, like species

richness, dissimilarity between communities depends highly on latitude. At lower latitudes, we found distinct urban and non-urban ant communities. At higher latitudes, similarity increased, resulting in ant communities with broad genus overlap. When considering both our analysis of species richness differences and community composition, we found that urbanisation did not have a uniform effect on diversity across latitude, and instead, had differential effects depending on geographic location. Our results suggest that the observed dampening effect of urbanisation on the latitude-diversity cline is mostly driven by the fact that tropical cities become relatively more species poor than high latitude cities, and urban tropical ant communities are quite different from nearby non-urban habitats, while at higher latitude, urban and non-urban ant communities are more similar, with neutral to positive impacts on richness and composition at higher latitudes. These findings are limited due to the resolution of our community metrics (genera, as opposed to species), thus the similarities in composition between high latitude urban and non-urban sites may be a result of relatively less genera to draw from in the regional pool (Economato et al., 2018). However, as many of the species within these genera have been found to do well in urban habitats (Buczkowski & Richmond, 2012; Menke et al., 2011; Perez & Diamond, 2019), including established urban exploiters, such *Tapinoma sessile*, and species of *Tetramorium* (Buczkowski & Richmond, 2012; Menke et al., 2010; Salyer et al., 2014), our analysis of community compositions may serve as an adequate proxy, although future research will benefit from species-level descriptions of diversity, quantifying species abundances, and standardising sample efforts.

With ongoing rapid urban expansion, (Cincotta et al., 2000; Luck, 2007; Seto et al., 2012), there is a critical need to understand how typical biogeographic patterns might be impacted by or interact with urbanisation. While this area of research is largely understudied, early evidence on the differential impact of urbanisation across latitude has been observed in insect morphology (Beasley et al., 2018). In cicadas, non-urban populations exhibited the typical relationship of increasing body size with latitude, whereas urban populations exhibited the opposite trend. Urban populations of cicadas at higher latitudes were larger relative to their non-urban counterparts, reversing the expected body size–latitude relationship (Beasley et al., 2018). Consistent with our findings, the direction and magnitude of the urbanisation effect vary geographically, with stronger detrimental effects at lower latitudes. Although more data are needed, it is possible that this interaction between urbanisation and geographic position could be widespread among taxa and biological responses.

We found that urbanisation alters global biodiversity patterns, but our work might also suggest important avenues of future research into the mechanisms underlying the latitude–diversity relationship. Climatic harshness of high latitude environments is one hypothesis for a mechanism underlying the latitude-diversity cline (Currie et al., 2004). Under this hypothesis, high latitude environments are species-poor due to limitations on performance and survival driven by low temperatures. In this context, cities provide a unique test of the climatic harshness hypothesis: on the cold end of the range of thermal performance, cities and their associated urban heat island effects might relax constraints imposed by low temperatures at high latitude

sites, whereas on the warm end of the range of thermal performance, cities might exacerbate costs of high temperatures leading species to overheat. This general pattern has been found to underlie differences in vulnerability of ectothermic species to global climate change. As global temperatures increase, stronger negative consequences on tropical biodiversity are expected, as many of these species currently live at the limits of their physiological tolerance (Deutsch et al., 2008; Huey et al., 2009; Sunday et al., 2014). The degree to which urban warming at high versus low latitudes explains the dampening of the latitude–diversity relationship in ants, and possibly other species, remains unclear, but nonetheless represents a directly testable hypothesis.

Unfortunately, in tropical areas, where species are at the greatest extinction risk from anthropogenic climate change (Deutsch et al., 2008; Huey et al., 2009; Tewksbury et al., 2008), urban development is accelerating in growth (Cincotta et al., 2000; Luck, 2007; Seto et al., 2012), often affecting rare and endemic species, and habitats important for ecosystem functioning (Pickett et al., 2011). This places urgency on studies examining the role of urbanisation in global biodiversity and identifying the mechanisms driving latitudinal variation in the effects of urbanisation. Moving forward, future investigations would benefit our understanding by identifying predictable trait responses and community assembly, to urban factors such as temperature, while simultaneously investigating these responses across broad geographic scales.

AUTHOR CONTRIBUTIONS

All authors helped developed the study and provided feedback throughout. Abe Perez, Lacy Chick, Sean Menke, and Niklas Sundebo Meldgaard collected data. Abe Perez conducted the analyses with assistance from Sarah Diamond. Abe Perez wrote the initial version of the manuscript, with important feedback and collaboration from Sarah Diamond, Lacy Chick, Sean Menke, Jean-Philippe Lessard, Nathan Sanders, Israel Del Toro, and Niklas Sundebo Meldgaard.

ACKNOWLEDGEMENTS

The authors thank Andrew Suarez, Jean Burns, Michael Benard, and two anonymous reviewers for their helpful comments that improved the manuscript.

CONFLICT OF INTEREST

The authors have no conflict of interests to declare.

DATA AVAILABILITY STATEMENT

The data that support the findings of this study are available upon request from the corresponding author.

ORCID

Abe Perez  <https://orcid.org/0000-0002-3568-1139>

Jean-Philippe Lessard  <https://orcid.org/0000-0002-7236-436X>

REFERENCES

- Arnan, X., Cerdá, X. & Retana, J. (2017) Relationships among taxonomic, functional, and phylogenetic ant diversity across the biogeographic regions of Europe. *Ecography*, 40, 448–457.

- Aronson, M.F.J., La Sorte, F.A., Nilon, C.H., Katti, M., Goddard, M.A., Lepczyk, C.A. et al. (2014) A global analysis of the impacts of urbanization on bird and plant diversity reveals key anthropogenic drivers. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20133330. <https://doi.org/10.1098/rspb.2013.3330>
- Baldock, K.C.R., Goddard, M.A., Hicks, D.M., Kunin, W.E., Mitschunas, N., Osgathorpe, L.M. et al. (2015) Where is the UK's pollinator biodiversity? The importance of urban areas for flower-visiting insects. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20142849. <https://doi.org/10.1098/rspb.2014.2849>
- Batty, M. (2008) The size, scale, and shape of cities. *Science*, 319, 769–771.
- Beasley, D.E., Penick, C.A., Boateng, N.S., Menninger, H.L. & Dunn, R.R. (2018) Urbanization disrupts latitude-size rule in 17-year cicadas. *Ecology and Evolution*, 8, 2534–2541. <https://doi.org/10.1002/ece3.3879>
- Bestelmeyer, B. (2000) Field techniques for the study of ground-dwelling ants: an overview, description, and evaluation. In: Agosti, D., Majer, J.D., Alonso, L.E. & Shultz, T.R. (Eds.) *Ants: standard methods for measuring and monitoring*. Washington DC, USA: Smithsonian Institution Press, pp. 125–145.
- Buczkowski, G. & Richmond, D.S. (2012) The effect of urbanization on ant abundance and diversity: a temporal examination of factors affecting biodiversity. *PLoS One*, 7, e41729.
- Cincotta, R.P., Wisniewski, J. & Engelman, R. (2000) Human population in the biodiversity hotspots. *Nature*, 404, 990–992. <https://doi.org/10.1038/35010105>
- Clergeau, P., Croci, S., Jokimäki, J., Kaisanlahti-Jokimäki, M.-L. & Dinetti, M. (2006) Avifauna homogenisation by urbanisation: analysis at different European latitudes. *Biological Conservation, Urbanization*, 127, 336–344. <https://doi.org/10.1016/j.biocon.2005.06.035>
- Currie, D.J., Mittelbach, G.G., Cornell, H.V., Field, R., Guégan, J.-F., Hawkins, B.A. et al. (2004) Predictions and tests of climate-based hypotheses of broad-scale variation in taxonomic richness. *Ecology Letters*, 7, 1121–1134. <https://doi.org/10.1111/j.1461-0248.2004.00671.x>
- Deutsch, C.A., Tewksbury, J.J., Huey, R.B., Sheldon, K.S., Ghalambor, C.K., Haak, D.C. et al. (2008) Impacts of climate warming on terrestrial ectotherms across latitude. *PNAS*, 105, 6668–6672. <https://doi.org/10.1073/pnas.0709472105>
- Dunn, R.R., Guenard, B., Weiser, M.D. & Sanders, N.J. (2010) Geographic gradients. In: *Ant ecology*. Oxford, UK: Oxford University Press, pp. 38–58.
- Economu, E.P., Narula, N., Friedman, N.R., Weiser, M.D. & Guénard, B. (2018) Macroecology and macroevolution of the latitudinal diversity gradient in ants. *Nature Communications*, 9, 1–8. <https://doi.org/10.1038/s41467-018-04218-4>
- Elvidge, C., Tuttle, B., Sutton, P., Baugh, K., Howard, A., Milesi, C. et al. (2007) Global distribution and density of constructed impervious surfaces. *Sensors*, 7, 1962–1979.
- Faeth, S.H., Bang, C. & Saari, S. (2011) Urban biodiversity: patterns and mechanisms: urban biodiversity. *Annals of the New York Academy of Sciences*, 1223, 69–81. <https://doi.org/10.1111/j.1749-6632.2010.05925.x>
- Gaston, K.J. (2000) Global patterns in biodiversity. *Nature*, 405, 220–227. <https://doi.org/10.1038/35012228>
- Ghalambor, C.K., Huey, R.B., Martin, P.R., Tewksbury, J.J. & Wang, G. (2006) Are mountain passes higher in the tropics? Janzen's hypothesis revisited. *Integrative and Comparative Biology*, 46, 5–17.
- Gibb, H., Dunn, R.R., Sanders, N.J., Grossman, B.F., Photakis, M., Abril, S. et al. (2017) A global database of ant species abundances. *Ecology*, 98, 883–884. <https://doi.org/10.1002/ecy.1682>
- Gibb, H., Sanders, N.J., Dunn, R.R., Watson, S., Photakis, M., Abril, S. et al. (2015) Climate mediates the effects of disturbance on ant assemblage structure. *Proceedings of the Royal Society B: Biological Sciences*, 282, 20150418. <https://doi.org/10.1098/rspb.2015.0418>
- Gippet, J.M.W., Mondy, N., Diallo-Dudek, J., Bellec, A., Dumet, A., Mistler, L. et al. (2017) I'm not like everybody else: urbanization factors shaping spatial distribution of native and invasive ants are species-specific. *Urban Ecosystem*, 20, 157–169. <https://doi.org/10.1007/s11252-016-0576-7>
- Grimm, N.B., Faeth, S.H., Golubiewski, N.E., Redman, C.L., Wu, J., Bai, X. et al. (2008) Global change and the ecology of cities. *Science*, 319, 756–760. <https://doi.org/10.1126/science.1150195>
- Grimm, N.B., Foster, D., Groffman, P., Grove, J.M., Hopkinson, C.S., Nadelhoffer, K.J. et al. (2008) The changing landscape: ecosystem responses to urbanization and pollution across climatic and societal gradients. *Frontiers in Ecology and the Environment*, 6, 264–272. <https://doi.org/10.1890/070147>
- Hawkins, B.A. (2001) Ecology's oldest pattern? *Trends in Ecology & Evolution*, 16, 470. [https://doi.org/10.1016/S0169-5347\(01\)02197-8](https://doi.org/10.1016/S0169-5347(01)02197-8)
- Helms, J. (2017) The flight ecology of ants (hymenoptera: Formicidae). *Myrmecological News*, 26, 19–30.
- Hill, M.J., Biggs, J., Thornhill, I., Briers, R.A., Gledhill, D.G., White, J.C. et al. (2017) Urban ponds as an aquatic biodiversity resource in modified landscapes. *Global Change Biology*, 23, 986–999. <https://doi.org/10.1111/gcb.13401>
- Hillebrand, H. (2004) On the generality of the latitudinal diversity gradient. *The American Naturalist*, 163, 192–211. <https://doi.org/10.1086/381004>
- Hodges, M.N. & McKinney, M.L. (2018) Urbanization impacts on land snail community composition. *Urban Ecosystem*, 21, 721–735. <https://doi.org/10.1007/s11252-018-0746-x>
- Huey, R.B., Deutsch, C.A., Tewksbury, J.J., Vitt, L.J., Hertz, P.E., Pérez, H. J.Á. et al. (2009) Why tropical forest lizards are vulnerable to climate warming. *Proceedings of the Royal Society of London B: Biological Sciences*, 276, 1939–1948. <https://doi.org/10.1098/rspb.2008.1957>
- Kaspari, M., Yuan, M. & Alonso, L. (2003) Spatial grain and the causes of regional diversity gradients in ants. *The American Naturalist*, 161, 459–477.
- Knop, E. (2016) Biotic homogenization of three insect groups due to urbanization. *Global Change Biology*, 22, 228–236. <https://doi.org/10.1111/gcb.13091>
- Kühn, I. & Klotz, S. (2006) Urbanization and homogenization – comparing the floras of urban and rural areas in Germany. *Biological Conservation, Urbanization*, 127, 292–300. <https://doi.org/10.1016/j.biocon.2005.06.033>
- Kusnezov, N. (1957) Numbers of species of ants in faunas of different latitudes. *Evolution*, 11, 298–299.
- Lach, L., Parr, C.L. & Abbott, K.L. (Eds.). (2010) *Ant ecology*. Oxford: Oxford University Press.
- Liu, Z., He, C., Zhou, Y. & Wu, J. (2014) How much of the world's land has been urbanized, really? A hierarchical framework for avoiding confusion. *Landscape Ecology*, 29, 763–771. <https://doi.org/10.1007/s10980-014-0034-y>
- Luck, G.W. (2007) A review of the relationships between human population density and biodiversity. *Biological Reviews*, 82, 607–645. <https://doi.org/10.1111/j.1469-185X.2007.00028.x>
- Luck, G.W. & Smallbone, L.T. (2010) Species diversity and urbanisation: patterns, drivers and implications. In: *Urban Ecology*. New York, USA: Cambridge University Press, pp. 88–119.
- McArdle, B.H. & Anderson, M.J. (2001) Fitting multivariate models to community data: a comment on distance-based redundancy analysis. *Ecology*, 82, 290–297.
- McGlynn, T.P. (1999) The worldwide transfer of ants: geographical distribution and ecological invasions. *Journal of Biogeography*, 26, 535–548. <https://doi.org/10.1046/j.1365-2699.1999.00310.x>
- Menke, S.B., Booth, W., Dunn, R.R., Schal, C., Vargo, E.L. & Silverman, J. (2010) Is it easy to be urban? Convergent success in urban habitats among lineages of a widespread native ant. *PLoS One*, 5(2), e9194.
- Menke, S.B., Guénard, B., Sexton, J.O., Weiser, M.D., Dunn, R.R. & Silverman, J. (2011) Urban areas may serve as habitat and corridors

- for dry-adapted, heat tolerant species; an example from ants. *Urban Ecosystem*, 14, 135–163. <https://doi.org/10.1007/s11252-010-0150-7>
- Moreau, C.S. & Bell, C.D. (2013) Testing the museum versus cradle tropical biological diversity hypothesis: phylogeny, diversification, and ancestral biogeographic range evolution of the ants. *Evolution*, 67, 2240–2257. <https://doi.org/10.1111/evo.12105>
- Niemelä, J. & Kotze, D.J. (2009) Carabid beetle assemblages along urban to rural gradients: a review. *Landscape and Urban Planning*, 92, 65–71. <https://doi.org/10.1016/j.landurbplan.2009.05.016>
- Nilon, C.H. (2011) Urban biodiversity and the importance of management and conservation. *Landscape and Ecological Engineering*, 7, 45–52. <https://doi.org/10.1007/s11355-010-0146-8>
- Oke, T.R. (1982) The energetic basis of the urban heat island. *Quarterly Journal of the Royal Meteorological Society*, 108, 1–24.
- Oksanen, J., Blanchet, F.G., Friendly, M., Kindt, R., Legendre, P., McGinn, D. et al. (2017) *vegan: community ecology package*. R package Version 2.4-3. <https://CRAN.R-project.org/package=vegan>
- Pautasso, M., Böhning-Gaese, K., Clergeau, P., Cueto, V.R., Dinetti, M., Fernández-Juricic, E. et al. (2011) Global macroecology of bird assemblages in urbanized and semi-natural ecosystems. *Global Ecology and Biogeography*, 20, 426–436.
- Perez, A. & Diamond, S.E. (2019) Idiosyncrasies in cities: evaluating patterns and drivers of ant biodiversity along urbanization gradients. *Journal of Urban Ecology*, 5, 1–10. <https://doi.org/10.1093/jue/juz017>
- Pickett, S.T.A., Cadenasso, M.L., Grove, J.M., Boone, C.G., Groffman, P.M., Irwin, E. et al. (2011) Urban ecological systems: scientific foundations and a decade of progress. *Journal of Environmental Management*, 92, 331–362. <https://doi.org/10.1016/j.jenvman.2010.08.022>
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D. & R-core Team. (2017) nlme: linear and nonlinear mixed effects models. *R Package Version*, 3(57), 1–89.
- R Core Team. (2018) *R: a language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing.
- Saari, S., Richter, S., Higgins, M., Oberhofer, M., Jennings, A. & Faeth, S.H. (2016) Urbanization is not associated with increased abundance or decreased richness of terrestrial animals - dissecting the literature through meta-analysis. *Urban Ecosystem*, 19, 1251–1264. <https://doi.org/10.1007/s11252-016-0549-x>
- Sadler, J., Bates, A., Hale, J. & James, P. (2010) Bringing cities alive: the importance of urban green spaces for people and biodiversity. In: *Urban ecology*. Cambridge: Cambridge University Press, pp. 230–260.
- Salyer, A., Bennett, G.W. & Buczkowski, G.A. (2014) Odorous house ants (*Tapinoma sessile*) as back-seat drivers of localized ant decline in urban habitats. *PLoS One*, 9(12), e113878.
- Sanders, N.J., Moss, J. & Wagner, D. (2003) Patterns of ant species richness along elevational gradients in an arid ecosystem. *Global Ecology and Biogeography*, 12, 93–102. <https://doi.org/10.1046/j.1466-822X.2003.00324.x>
- Santos, M.N. (2016) Research on urban ants: approaches and gaps. *Insectes Sociaux*, 63, 359–371. <https://doi.org/10.1007/s00040-016-0483-1>
- Seto, K.C., Güneralp, B. & Hutyra, L.R. (2012) Global forecasts of urban expansion to 2030 and direct impacts on biodiversity and carbon pools. *Proceedings of the National Academy of Sciences*, 109, 16083–16088.
- Sunday, J.M., Bates, A.E., Kearney, M.R., Colwell, R.K., Dulvy, N.K., Longino, J.T. et al. (2014) Thermal-safety margins and the necessity of thermoregulatory behavior across latitude and elevation. *Proceedings of the National Academy of Sciences of the United States of America*, 111, 5610–5615. <https://doi.org/10.1073/pnas.1316145111>
- Tewksbury, J.J., Huey, R.B. & Deutsch, C.A. (2008) ECOLOGY: putting the heat on tropical animals. *Science*, 320, 1296–1297. <https://doi.org/10.1126/science.1159328>
- Thompson, B. & McLachlan, S. (2007) The effects of urbanization on ant communities and myrmecochory in Manitoba, Canada. *Urban Ecosystem*, 10, 43–52. <https://doi.org/10.1007/s11252-006-0013-4>
- United Nations Department of Economic and Social Affairs. (2015) *World urbanization prospects: the 2014 revision*. New York, NY: United Nations Department of Economic and Social Affairs, Population Division, p. 41.
- Van Nuland, M.E. & Whitlow, W.L. (2014) Temporal effects on biodiversity and composition of arthropod communities along an urban–rural gradient. *Urban Ecosystem*, 17, 1047–1060. <https://doi.org/10.1007/s11252-014-0358-z>
- Wang, Z., Brown, J.H., Tang, Z. & Fang, J. (2009) Temperature dependence, spatial scale, and tree species diversity in eastern Asia and North America. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 13388–13392. <https://doi.org/10.1073/pnas.0905030106>
- Wang, Z., Fang, J., Tang, Z. & Lin, X. (2011) Patterns, determinants and models of woody plant diversity in China. *Proceedings of the Royal Society B: Biological Sciences*, 278, 2122–2132. <https://doi.org/10.1098/rspb.2010.1897>
- Ward, P.S. (2010) Taxonomy, phylogenetics, and evolution. In: Lach, L., Parr, C. & Abbott, K. (Eds.) *Ant ecology*. Oxford: Oxford University Press, p. 402.
- Wenzel, A., Grass, I., Belavadi, V.V. & Tschamtkke, T. (2020) How urbanization is driving pollinator diversity and pollination – a systematic review. *Biological Conservation*, 241, 108321. <https://doi.org/10.1016/j.biocon.2019.108321>
- Willig, M.R., Kaufman, D.M. & Stevens, R.D. (2003) Latitudinal gradients of biodiversity: pattern, process, scale, and synthesis. *Annual Review of Ecology, Evolution, and Systematics*, 34, 273–309. <https://doi.org/10.1146/annurev.ecolsys.34.012103.144032>
- Winter, M., Schweiger, O., Klotz, S., Nentwig, W., Andriopoulos, P., Arianoutsou, M. et al. (2009) Plant extinctions and introductions lead to phylogenetic and taxonomic homogenization of the European flora. *Proceedings of the National Academy of Sciences of the United States of America*, 106, 21721–21725. <https://doi.org/10.1073/pnas.0907088106>
- Youngsteadt, E., Ernst, A.F., Dunn, R.R. & Frank, S.D. (2017) Responses of arthropod populations to warming depend on latitude: evidence from urban heat islands. *Global Change Biology*, 23, 1436–1447. <https://doi.org/10.1111/gcb.13550>

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

Table S1: List of studies used in analyses, including habitat designation.

Table S2: Estimates and statistical significance of the predictors habitat (urban vs. non-urban), impervious surface area (ISA), absolute latitude, and their interactions on ant species richness from a linear mixed-effects model. Estimates show differences from non-urban habitats. Significance was assessed using likelihood ratio tests. Significant *p* values in bold.

Table S3: Estimates and statistical significance of the predictors absolute latitude and impervious surface area (ISA), from a linear regression, on species richness differences (urban minus non-urban species richness).

How to cite this article: Perez, A., Chick, L., Menke, S., Lessard, J.-P., Sanders, N., Del Toro, I. et al. (2022) Urbanisation dampens the latitude-diversity cline in ants. *Insect Conservation and Diversity*, 15(6), 763–771. Available from: <https://doi.org/10.1111/icad.12598>