

Dispersal barriers and climate determine the geographic distribution of the helicopter damselfly *Mecistogaster modesta*

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Abstract

1. Species' ranges are typically constrained by the interplay of physical barriers to dispersal, environmental requirements such as suitable climatic conditions and biotic constraints such as from predation or competition. However, teasing apart the relative importance of these constraints in determining species distributions still represents a major challenge for ecologists.
2. The Neotropical damselfly *Mecistogaster modesta* (Coenagrionidae: Odonata) inhabits wet and moist forests in mainland Central America and north-western South America. This habitat specialist spends its larval development exclusively in tank bromeliads, where it acts as a keystone predator within the aquatic food web. Although tank-forming bromeliads occur from the southern United States throughout most of South America, *M. modesta* is absent from the Caribbean islands and South America south-east of the Andes mountain chain.
3. We employed species distribution models to explore the relative importance of physical barriers (Andes mountain range and oceanic barriers), climate (mean annual temperature and annual precipitation) and biotic interactions (competition from other bromeliad-dwelling odonates) in limiting the geographic distribution of *M. modesta*.
4. We found that dispersal barriers strongly limit the geographic distribution of *M. modesta*. In addition, its range is restricted by low temperatures and low precipitation. Competition from other bromeliad-dwelling odonates was not important in limiting the damselfly's range. Because of the physical barriers to dispersal, *M. modesta* does not occupy its full potential geographic range. Specifically, our model predicted suitable habitat on the Caribbean islands and throughout most of South America, where the species is currently absent.
5. These findings have important conservation implications, particularly as the aridification of rainforests and subsequent localised extinctions due to climate change continue. On the other hand, the species may respond to warming temperatures by tracking climate to higher elevations, with subsequent effects on naïve high-elevation bromeliad food webs. An upwards migration could also increase the probability of *M. modesta* overcoming the dispersal barrier presented by the Andes, enabling the damselfly to invade large areas of suitable habitat in South America.

KEYWORDS

Bromeliagrion, dispersal limitation, physiological niche, Pseudostigmatidae, tank bromeliad

1 | INTRODUCTION

Damselflies and dragonflies (Odonata) are among the most ancient winged insects on Earth (~300 MYA: Ingley, Bybee, Tennesen, Whiting, & Branham, 2012). As both adults and larvae typically occupy high trophic positions, these insects are often used as indicators of aquatic and terrestrial ecosystem health (Collins & McIntyre, 2015). Odonates possess some of the best dispersal capabilities of all insects (Sánchez-Herrera & Ware, 2012), yet these acrobatic flyers are not found everywhere. Teasing apart the relative importance of factors that determine the geographic distributions of odonates (Collins & McIntyre, 2015), as well as of organisms in general (De Araújo, Marcondes-Machado, & Costa, 2014; Endler, 1982), still represents a major challenge for ecologists.

Major mountain ranges have led to the isolation and subsequent diversification of plants (e.g., Antonelli, Nylander, Persson, Sanmartin, & Tiffney, 2009) and animals, including invertebrates (e.g., De-Silva, Elias, Willmott, Mallet, & Day, 2016; Von Oheimb et al., 2013) and birds (e.g., Graham, Parra, Rahbek, & McGuire, 2009). Similarly, large expanses of water such as oceans and great lakes represent major dispersal barriers to most terrestrial organisms (MacDonald, 2003) and can restrict the geographic ranges of even good dispersers, such as winged insects (e.g., yellow-faced bumble bee: Jha, 2015). Such direct physical barriers may limit the geographic distributions of odonates, and indeed, their range edges often coincide with mountain ranges and oceans (Wellenreuther, Larson, & Svensson, 2012). However, geographic barriers usually do not fully explain the geographic range limits of odonates.

The constrained geographic ranges of odonates may also be a function of their sensitivity to environmental conditions. At large spatial scales, climate, particularly temperature and precipitation, appears to ultimately determine the physiological niche of organisms (Pearson & Dawson, 2003), including odonates (Collins & McIntyre, 2015). Temperature determines, among other things, thermoregulation proficiency (De Marco, Latini, & Resende, 2005), flight performance of adults (Dingemans & Kalkman, 2008; Samejima & Tsubaki, 2010), development rates of larvae (Braune, Richter, Söndgerath, & Suhling, 2008; Hassall, Thompson, French, & Harvey, 2007; Lutz, 1968; Pickup & Thompson, 1990; Richter, Suhling, Müller, & Kern, 2008), time to emergence (Hassall et al., 2007; Richter et al., 2008) and voltinism (i.e., the number of generations completed within 1 year in the field: Braune et al., 2008). Precipitation, on the other hand, is strongly linked to hydroperiod in lentic waters (Collins et al., 2014) and thus determines environmental suitability for oviposition by odonates. In addition, low precipitation and associated increases in drought lengths and/or frequencies can adversely affect odonate larvae (Amundrud & Srivastava, 2015; Amundrud & Srivastava, 2016; Ball-Damerow, M'Gonigle, & Resh, 2014a,b).

Apart from dispersal limitation and abiotic constraints, biotic interactions such as predation and competition may also limit the distributions of odonates (Collins & McIntyre, 2015). For example, the presence of predatory fish is strongly linked to the occurrence of some odonate species in ponds (McGuffin, Baker, & Forbes, 2006). In temporary waters where fish are absent, other odonate species represent strong biotic controls (e.g., Benke, 1978; Fincke, 1994; Johnson, Crowley, Bohanan, Watson, & Martin, 1985). In such systems, intraguild predation (where predators with shared prey kill and eat each other: Polis, Myers, & Holt, 1989) and cannibalism are the main biotic constraints (e.g., Benke, 1978; Sutari, Rantala, Salmela, & Suhonen, 2004). Biotic interactions can also limit distributions of odonates through the "ghost of competition past" (Worthen & Horacek, 2015), where current geographical limits of species reflect the historical avoidance of competition with other organisms (Connell, 1980). Although important at the local scale, biotic interactions are often considered to be negligible in affecting species distributions at large geographical scales (Eltonian noise hypothesis: Soberón & Nakamura, 2009). Nevertheless, recent work suggests that biotic interactions can be important in affecting species distributions even at large spatial scales (e.g., Boulangeat, Gravel, & Thuiller, 2012; De Araújo et al., 2014; Heikkinen, Luoto, Virkkala, Pearson, & Körber, 2007).

The realised geographic distributions of odonates are likely determined by the interplay of physical barriers limiting their dispersal, environmental requirements and biotic constraints (see BAM [biotic, abiotic and migration] diagram in Soberón, 2007). The BAM model (Soberón, 2007) posits that the range that a species fills should represent all areas within the dispersal ability of the species (M) with suitable abiotic (A) and biotic (B) conditions. Species distribution models (SDMs) can be valuable in teasing apart these factors in limiting odonate distributions (Collins & McIntyre, 2015), especially if the relative contributions of the main factors conceptualised in the BAM model are well understood, or at least hypothesised (Saupe et al., 2012). However, few, if any, studies have evaluated the combined effects of climate, physical barriers and biotic constraints on odonate ranges.

Here, we employ SDMs to explore the factors that limit the geographical distribution of the Neotropical damselfly *Mecistogaster modesta* (Coenagrionidae: Odonata). *M. modesta* oviposits its eggs exclusively in epiphytic bromeliads (Ingley et al., 2012), where the larvae feed on other insect larvae (Srivastava, 2006). Adults feed on orb-weaving spiders, which they pluck from webs (Hedström & Sahlén, 2001; Ingley et al., 2012). Although tank-forming bromeliads occur from the southern United States (latitude ~30°N) to almost the southern tip of South America (latitude ~45°S: Benzing, 2000), *M. modesta* is limited to mainland Central America and north-western South America, inhabiting wet and moist forests from Colombia

and Venezuela to Mexico–Belize (Hedström & Sahlén, 2001). Throughout much of its range, *M. modesta* is the only odonate species associated with bromeliads, although there may be some overlap with other bromeliad-dwelling odonates in the genus *Bromeliagrion* (Coenagrionidae) towards the southern limit of its range (see Figure 1 and Supporting Information). Within bromeliads, *M. modesta* nymphs have large top-down effects on the bromeliad ecosystem that eclipse the effects of any other invertebrate species. For example, *M. modesta* larvae have been shown to reduce abundances of other invertebrates by 25%–90% (Hammill, Atwood, & Srivastava, 2015; Srivastava, 2006) and decomposition by 20%–50% (Atwood et al., 2013; Srivastava, 2006), increase nitrogen uptake by the bromeliad by 1200% (Ngai & Srivastava, 2006) and change CO₂ flux by up to 200% (Atwood et al., 2013; Hammill, Atwood, & Srivastava, 2015). Bromeliads that contain *M. modesta* have fundamentally different biomass pyramids and mosquito communities than bromeliads that do not (Hammill, Atwood, Corvalan, & Srivastava, 2015; Petermann et al., 2015). Determining which factors limit the geographic distribution of this odonate species is therefore essential to understanding spatial patterns in the structure and functioning of bromeliad food webs in Central America, and how these food webs may change under altered climate.

We used SDMs to explore the combined effects of climate, physical barriers and biotic constraints on *M. modesta*. SDMs have been widely applied for freshwater species, to explore matters as diverse as assessing the impacts of climate change (e.g., benthic stream macroinvertebrates: Domisch, Jähnig, & Haase, 2011), predicting suitable habitat for threatened species (e.g., freshwater turtle: Costa et al., 2015) and predicting the spatial distribution of invasive species (e.g., piscivorous chub: Sato et al., 2010). A detailed review

on the use of SDMs to model odonate distributions has been conducted by Collins and McIntyre (2015). We employed SDMs to reveal the relative importance of physical barriers (Andes mountain range and oceanic barriers), climate (temperature and precipitation) and biotic interactions (competition from other bromeliad-dwelling damselflies). If our model predicts no or little suitable habitat beyond the physical barriers constraining the range of *M. modesta*, it would indicate that climate and/or biotic constraints are the major factors limiting the damselfly's range. In contrast, if our model predicts suitable habitat on the islands and/or south-east of the Andes, it would suggest that *M. modesta* is limited by dispersal barriers. As there are neither obvious physical barriers nor other bromeliad-dwelling odonates towards the northern range limits of *M. modesta*, we expect climatic constraints to be the limiting factors towards the north.

2 | METHODS

2.1 | Data collection

We obtained occurrence records of *M. modesta* from several online databases, including the Global Biodiversity Information Facility (www.gbif.org), Biodiversity and Environmental Resource Data System of Belize (www.biodiversity.bz), Smithsonian National Museum of Natural History (www.mnh.si.edu) and Odonata Central (www.odonatacentral.org). We attained additional records from members of the Bromeliad Working Group (<http://www.zoology.ubc.ca/~srivast/bwg/researchers.html>), museum curators, known experts of Odonata and published studies on invertebrates inhabiting bromeliad phytotelmata. We also included absence records as sites where at least 20 bromeliads were inspected and no *M. modesta* larvae were found.

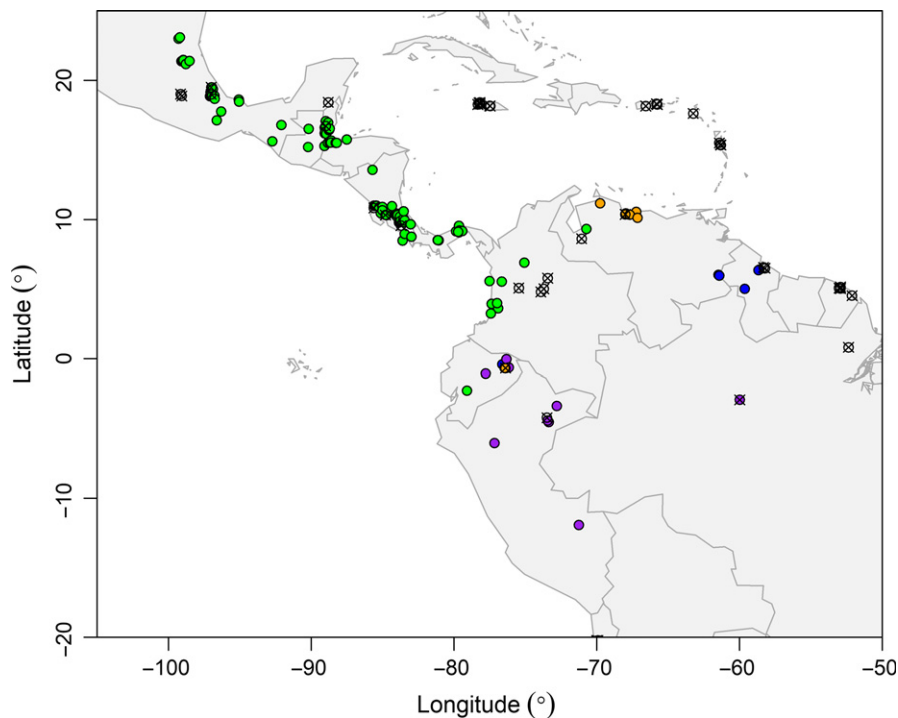


FIGURE 1 Map showing the location of presence and absence records of *Mecistogaster modesta*, as well as presence records of the three potential competitor species. Coloured dots show occurrence records of *M. modesta* (green), *Bromeliagrion beebanum* (blue), *Bromeliagrion rehni* (purple) and *Bromeliagrion fernandezianum* (orange). Empty dots with black crosses show *M. modesta* absence records

When no exact coordinates were available, we estimated the geographic coordinates and the associated error according to the point-radius method (Wieczorek, Guo, & Hijmans, 2004) using an online georeferencing calculator (<http://manisnet.org/gc.html>). We only included records with a geographical uncertainty of radius less than 5 km, resulting in a data set consisting of 101 presence and 52 absence records for *M. modesta* (Figure 1). The complete data set is available on Dryad Digital Repository (<https://doi.org/10.5061/dryad.8tp8n>).

2.2 | Variable selection

To examine the importance of dispersal in governing the distribution of *M. modesta*, we created a single binary “barrier” variable that indicated whether a record was collected from within versus beyond the hypothesised dispersal barriers represented by the Pacific and Atlantic oceans and the Andes mountain range. Specifically, the layer we created defined grid cells as “beyond barriers” (value = 0) when grid cells were south-east of the summit of the Andes or more than 10 km offshore of the mainland, or “within barriers” (value = 1) if in the rest of the terrestrial study area.

To examine the importance of climate, we obtained 19 bioclimatic variables from the WorldClim database at 2.5 arc-minutes resolution (Hijmans, Cameron, Parra, Jones, & Jarvis, 2005), which roughly corresponds to a 5-km resolution near the tropics. To select meaningful climatic predictor variables in our model, we first reduced our data set by removing all absence records from the islands and south-east of the Andes, as we a priori hypothesised that *M. modesta* cannot disperse to these areas because of dispersal barriers. Including these absences could lead to erroneous predictions, as absences from habitats due to dispersal barriers, but with suitable climate, would bias a model that predicts species occurrence from climate (Peterson et al., 2011). We then estimated and ranked relative variable importance as deviance explained for the 19 climate variables by predicting *M. modesta* occurrence for each of the climate variables separately using logistic generalised linear models (GLMs). Next, we examined the correlation between all possible variables to ensure that variables were not highly correlated ($r > .8$). This procedure led us to choose “annual mean temperature” (bio1) and “annual precipitation” (bio12), as these variables exhibited a high importance (they ranked first and fourth, respectively) and a low correlation ($r = .50$). In addition, this choice is consistent with the known physiological importance of temperature and precipitation to *M. modesta* (Amundrud and Srivastava, unpublished data). For both climatic variables, we compared the fitted curves of two polynomial logistic models (first degree and second degree, respectively) to a smooth spline. As the simpler curves (first-degree predictor variable) represented a closer fit to the data in both cases, we used first-degree predictor variables for bio1 and bio12 as climatic predictors of *M. modesta* occurrence in our final models.

Interacting species have been included as predictor variables in SDMs as either occurrence records or as an input layer of their estimated occurrence or habitat suitability (De Araújo et al., 2014; Gianini, Chapman, Saraiva, Alves-dos-Santos, & Biesmeijer, 2013). Here

we implemented the latter approach to examine whether competition determines the geographic distribution of *M. modesta* using the modelled distributions of three of its potential competitors: *Bromeliagrion bebeanum*, *B. fernandezianum* and *B. rehni*. We focused on those species because they are present in the north of South America, so their ranges may overlap with that of *M. modesta* (Figure 1). Other bromeliad-dwelling odonate species have too few records or occur too far from the known range of *M. modesta*, making competition unlikely. Because there are few presence records for these *Bromeliagrion* species (6, 6 and 11, respectively; Figure 1), we performed SDMs with Maxent version 3.2.1 (Phillips, Anderson, & Schapire, 2006), a widely used algorithm for presence-only data that performs better than others when the sample size is small (Hernandez, Graham, Master, & Albert, 2006; Wisz et al., 2008). For each competitor species, we included the habitat suitability scores obtained from the Maxent model as a continuous variable. In addition, we created variables for all possible combinations of competitor species whereby, for a given grid cell, the highest suitability value among the two (or three) competitor models was kept, resulting in seven possible competitor layers (the three competitor species individually, the three pairwise combination and all three competitor species combined). The results were qualitatively identical for all seven competitor layers; thus, we only report the results of the model in which the competition layer represents all three competitor species. This layer estimates the suitability of the habitat for at least one putative competitor of *M. modesta*, even if the identity of this competitor changes geographically. The detailed methods and results of the competitor models are listed in the Supporting Information.

2.3 | Species distribution models

We employed logistic GLMs to explore the relative importance of physical dispersal barriers, climate and competition in determining the geographic distribution of *M. modesta*. We chose GLMs because of their relatively high predictive power relative to other modelling approaches, as our goal was to predict *M. modesta* occurrence from these abiotic and biotic variables. Because it is crucial that the absence data used to train a SDM are limited to geographic areas within the dispersal ability of the species (i.e., within M in the BAM model: Peterson et al., 2011), our modelling approach consisted of two steps: (1) to statistically test our expectation that the ocean and Andes represent effective dispersal barriers (and thus, the absences on islands and the mainland south-east of the Andes represent records from areas outside of M [migration] in the BAM model but within A [abiotic] U B [biotic]); and, in the case that the model confirms that these absence records lie outside the area of dispersal capacity of *M. modesta*, (2) to predict *M. modesta* occurrence from climate and competition on a model trained on presence/absence records that lie within the area of dispersal capacity of the species (i.e., on the reduced data set excluding absence records on islands and south-east of the Andes, or within M in the BAM model).

To examine whether dispersal barriers limit the distribution of *M. modesta*, we employed an “across-barrier” model as a logistic

regression on the complete *M. modesta* data set (i.e., including the absence records from the islands and south-east of the Andes). As explanatory variables, we included the two climatic variables ("mean annual temperature" and "annual precipitation"), their interaction, the pooled competition variable and the binary "barrier" variable. We used the combined competitor variable (generated from all three competitor species) as described earlier. We used stepwise regression (function "step" in R [R Core Team, 2015]) for model simplification.

Because the distribution of *M. modesta* was strongly limited by the oceanic and mountain barriers (see Results), we employed a second "within-barrier" model that we trained on presence/absence records within the dispersal area (i.e., within M of BAM) of the damselfly. Training our model using records within M reduced the data set to 101 presences and 18 absences. As above, we used a logistic GLM to predict the probability of *M. modesta* occurrence from the two climatic variables, their interaction and the combined competition variable, followed by stepwise regression.

We performed a 10-fold cross-validation to check for model performance and robustness, using the R package DAAG (Maindonald & Braun, 2015). To calculate threshold-dependent model performance indices, we chose the threshold to maximise Kappa using the *PresenceAbsence* package (Freeman & Moisen, 2008) in R.

3 | RESULTS

The "across-barrier" analysis revealed that dispersal barriers limit the geographic distribution of *M. modesta*, as the barrier variable and the two climatic variables (bio1 and bio12) were significant predictors of the damselfly's occurrence (Table 1A). The competition variable and the interaction term of bio1 × bio12 were removed from the model by stepwise regression. The total variance explained by the model was 71.6%, and a 10-fold cross-validation established model robustness (Table 1B).

The "within-barrier" analysis revealed that climatic constraints are the most important limiting factors of *M. modesta* occurrence within the potential dispersive area of the species (Table 2A). As in

the "across-barrier" model, the interaction of bio1 × bio12 and the competition variable were removed from the model by stepwise regression. The total variance explained by the final model was 45%, and a 10-fold cross-validation showed adequate model robustness (Table 1B). A closer examination of the climatic constraints on *M. modesta* occurrence revealed that the species is limited by low temperatures and dry conditions, as rises in annual mean temperature (bio1) and annual precipitation (bio12) significantly increase the predicted probability of *M. modesta* occurrence (Figures 2a,b). Specifically, the mean annual temperature and precipitation for which our model predicts a 50% probability of *M. modesta* occurrence is 16.22°C (±0.95°C SE) and 1,091 mm (±217 mm SE), respectively (Figures 2a,b).

The predicted realised geographic distribution of *M. modesta* encompasses most of Central America (except at high elevations) and the northern parts of South America, spanning from southern Mexico below ~ 20°N (and further north at both of Mexico's coasts) to the north-eastern side of the Andes mountain range in South America (from east Venezuela to Ecuador and possibly into Peru; Figure 3). However, the potential geographic distribution predicted by our model spans far into South America to ~ 30°S and includes the Caribbean islands, suggesting that suitable habitat for *M. modesta* exists beyond the physical barriers represented by the ocean and Andes mountain range (Figure 4).

4 | DISCUSSION

Physical barriers to dispersal and climatic constraints determined the distribution of *M. modesta* in our study, but competition from other bromeliad-dwelling odonates was not important. In particular, we identified two dispersal barriers: oceanic distances in excess of 10 km and the Andes mountain chain, which exclude *M. modesta* from the Caribbean islands and from much of South America. In addition, annual mean temperature and annual precipitation were also key factors limiting the geographic distribution of *M. modesta*. These climatic constraints excluded *M. modesta* from high elevations (too cold), as well as from latitudes above its northern range

TABLE 1 Fit of simplified "across-barrier" model to the full data set of presence-absence records. Data to train the model included absences outside the hypothesised area of dispersal. The initial model included dispersal barriers, climatic constraints (annual mean temperature [bio1] and annual precipitation [bio12], as well as their interaction) and biological constraints (competitors). Competition and the bio1 × bio12 interaction terms were removed from the model by stepwise regression. (A) ANOVA table after stepwise regression. (B) Model performance indices and 10-fold cross-validation (CV)

(A)	df	Deviance	Residual df	Residual Deviance	p-Value		
NULL			152	196.13			
bio1	1	13.57	151	182.56	<.001		
bio12	1	12.89	150	169.67	<.001		
Barrier	1	114.05	149	55.62	<.001		
(B)	Threshold	PCC	Sensitivity	Specificity	Kappa	AUC	TSS
Model	0.45	0.95	0.99	0.87	0.88	0.97	0.86
10-fold CV	0.45	0.93	0.97	0.85	0.84	0.96	0.82

TABLE 2 Fit of simplified “within-barrier” model to the reduced data set of presence–absence records. Data to train the model did not include absences outside the hypothesised area of dispersal. The initial model included climatic constraints (annual mean temperature [bio1] and annual precipitation [bio12], as well as their interaction) and biological constraints (competitors). Competition and the bio1 × bio12 interaction terms were removed from the model by stepwise regression. (A) ANOVA table after stepwise regression. (B) Model performance indices and 10-fold cross-validation (CV)

(A)	df	Deviance	Residual df	Residual deviance	p-Value		
NULL			118	101.12			
bio1	1	36.44	117	64.69	<.001		
bio12	1	9.07	116	55.62	.002		
(B)	Threshold	PCC	Sensitivity	Specificity	Kappa	AUC	TSS
Model	0.57	0.92	0.97	0.67	0.68	0.93	0.64
10-fold CV	0.57	0.91	0.96	0.61	0.61	0.85	0.57

FIGURE 2 Probability of occurrence of *Mecistogaster modesta* for (a) annual mean temperature (bio1) and (b) annual precipitation (bio12). Empty circles represent presence (at 1) and absence (at 0) records of *M. modesta*. Lines represent the predicted probability of *M. modesta* occurrence from logistic regression models

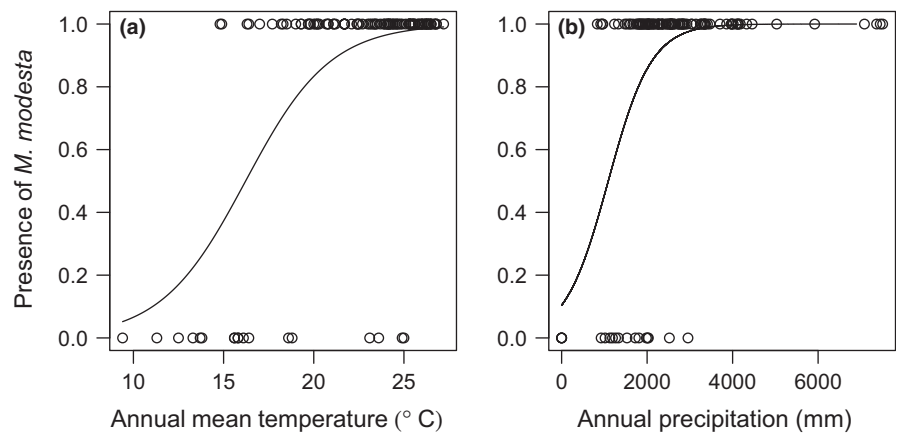
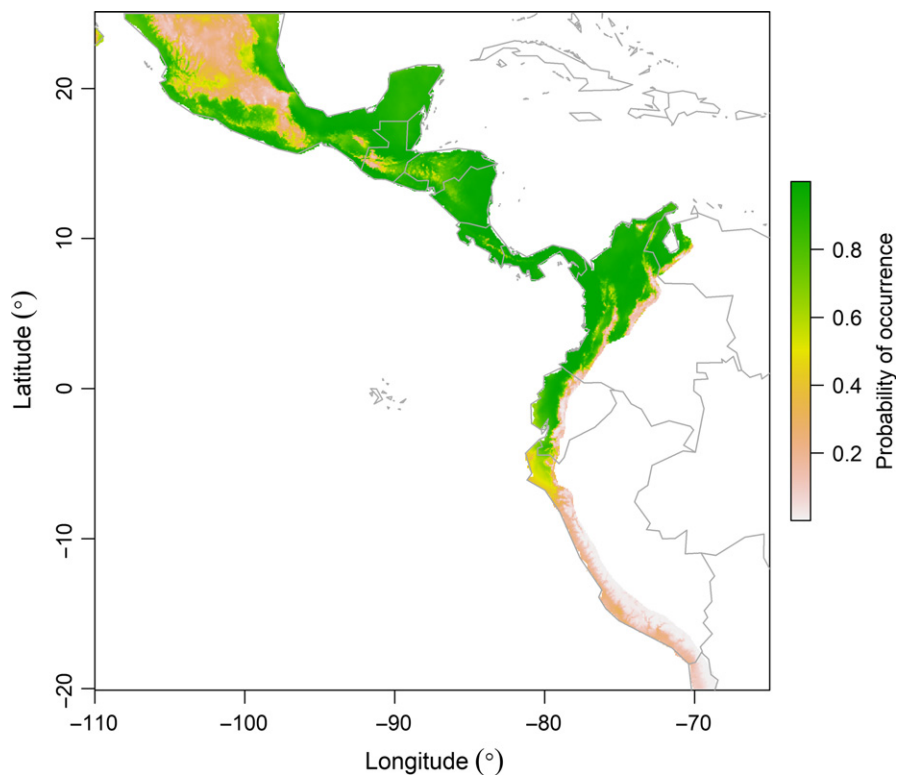


FIGURE 3 The predicted realised geographic distribution of *Mecistogaster modesta* (white to green colour scale indicates the probability of occurrence of *M. modesta*). This species distribution model is restricted to areas that are within the dispersal ability of the damselfly



edge in Mexico (too dry) and from west of the Andes (too dry and/or too cold; Figure 3). As dispersal barriers exclude *M. modesta* from suitable habitat on the Caribbean islands and south-east

of the Andes (Figure 3), our study indicates that this damselfly does not occupy its full potential geographic distribution (Figure 4).

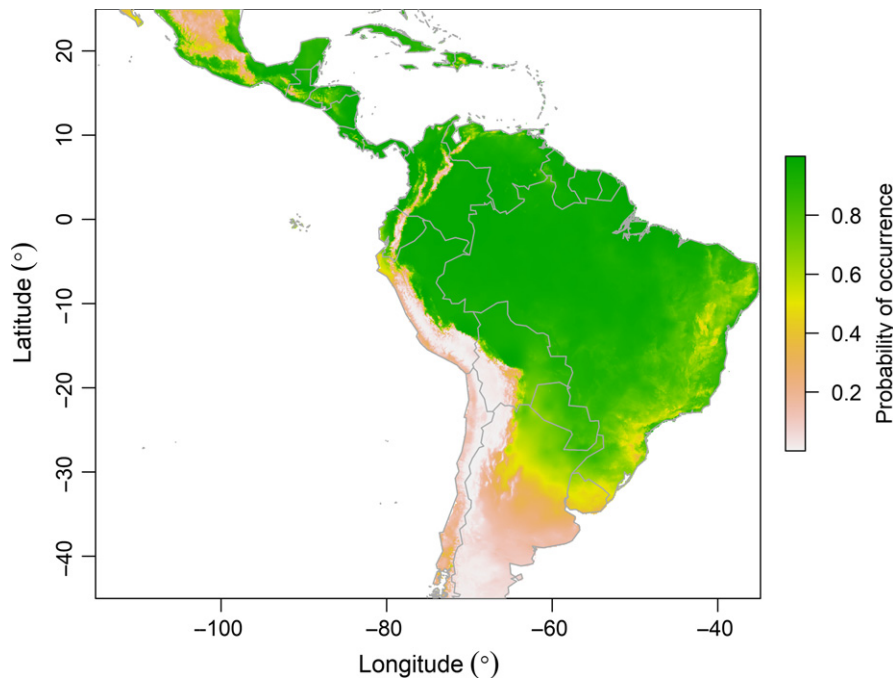


FIGURE 4 The predicted potential geographic distribution of *Mecistogaster modesta* (white to green colour scale indicates the probability of occurrence of *M. modesta*). Although the damselfly is not currently present on islands and east of the Andes, our model predicts that the climate there is suitable for the damselfly

Mecistogaster modesta is unlikely to occupy its full potential geographic niche, as our “across-barrier” analysis predicted suitable habitat on the Caribbean islands and south-east of the Andes. We conclude that *M. modesta*, like other Neotropical animals (Emmons & Feer, 1997), has not been able to cross the ocean expanse between the Central American mainland and the Caribbean islands to fill its potential range, consistent with marine barriers limiting animal distributions (MacDonald, 2003; Smith, 2009), even for taxa with good dispersal capabilities such as winged insects (Jha, 2015). In addition, the geographic distribution of *M. modesta* is constrained by the Andes mountain range, which excludes it from suitable habitat in much of South America (Figure 4). This is not surprising, as the Andes represent a significant barrier for many organisms including plants (e.g., Antonelli et al., 2009; Givnish et al., 2016), insects (e.g., De-Silva et al., 2016) and birds (e.g., Graham et al., 2009). It is likely that this mountain range represents a barrier to *M. modesta* because of unfavourable environmental conditions at high elevations, and indeed, Odonata richness often decreases with increasing elevations (e.g., Ecuadorian Andes: Jacobsen, 2003; S. L. Amundrud and D. S. Srivastava, personal observation). However, our analysis does suggest that potentially suitable habitat corridors exist through the Andes, notably in east-central Colombia and north-west Venezuela (Figure 4). It is possible that *M. modesta* has not successfully migrated through these low-elevation corridors simply because the habitat conditions there are not suitable despite a suitable climate (e.g., bromeliads or primary forest may be absent). Behavioural tendencies of *M. modesta* to avoid open areas may be more important than its ability to disperse, consistent with the discovery that dispersal behaviour is more important in predicting odonate range size than is dispersal capacity (McCauley, Davis, Werner, & Robeson, 2014). Indeed, biological corridors are also inefficient for the giant tree-hole breeding damselfly *Megaloprepus caerulatus*

(Pseudostigmatidae), which is sensitive to habitat fragmentation and does not travel through open areas (Khazan, 2014). However, it is important to note that odonates in the genus *Bromeliagrion* that do fill the bromeliad niche east of the Andes may occur across these physical barriers (Supporting Information), although too few records exist to make accurate predictions of their exact ranges. Any behavioural constraints of *M. modesta* that impede it from passing through such corridors may thus not apply to bromeliad-dwelling odonates in general.

In addition to physical barriers, climatic constraints were important factors limiting the geographic range of *M. modesta*, excluding the species from cold and dry areas. Although temperature and precipitation together affect water levels in bromeliads (i.e., high temperatures and low precipitation lead to the driest conditions in bromeliads), we did not find a significant interaction of precipitation and temperature (the interaction term was removed from the models by stepwise regression). Furthermore, damselflies were restricted by low temperatures rather than the high temperatures that would be associated with faster evaporation rates. Instead, both annual mean temperature and annual precipitation had strong individual positive effects on the probability of *M. modesta* occurrence (Figures 2a,b). Direct positive physiological effects of temperature on *M. modesta* thus appear to be more important than indirect negative effects of temperature by affecting the hydroperiod of bromeliads, consistent with studies showing that odonate occurrence (Ball-Damerow et al., 2014a) and richness (Jacobsen, 2003) increases with higher temperatures. Our finding that low precipitation limited *M. modesta* occurrence is also not surprising, as experimental evidence suggests that *M. modesta* larvae are disproportionately affected by drought (Amundrud & Srivastava, 2015, 2016), which results from low precipitation in bromeliads (Zotz & Thomas, 1999). Other studies have also found negative effects of low precipitation and drought on odonates

(e.g., Ball-Damerow et al., 2014a,b), particularly for those species that are habitat specialists (Ball-Damerow et al., 2014a).

Biotic factors were not important in limiting the distribution of *M. modesta*. However, the competition layer used in our models correlated with the layer representing dispersal barriers, and such correlations can result in biotic interactions being masked (Godsoe, Franklin, & Blanchet, 2017). Still, closely related species of giant damselflies that breed in water-filled tree holes do coexist despite strong intraguild predation, because large larvae kill smaller ones independently of species identity, ensuring that competitive dominance is more a function of larval size than species identity (Fincke, 1994). Similarly, our study shows that in South America, the ranges of the three bromeliad-dwelling damselflies (*Bromeliagrion bebeanum*, *B. fernandezianum* and *B. rehni*) do overlap (see Supporting Information), suggesting that competition does not constrain the distributions of those species at a large spatial scale.

To summarise, both physical barriers to dispersal and climatic constraints were important limiting factors of the geographic distribution of *M. modesta*, while competition from other bromeliad-dwelling odonates was not. Our finding that the distribution of this damselfly is strongly linked to climate has important conservation implications, particularly as aridification of rainforests due to climate change continues (Brodie, Post, & Laurance, 2012). Conversely, this species may benefit from rising temperatures by tracking climate to higher elevations. The introduction of this novel predator to high-elevation systems would have strong effects on naïve high-elevation bromeliad food webs. An upwards migration by *M. modesta* could also increase the probability of this species overcoming the dispersal barrier presented by the Andes, enabling it to invade large areas of suitable habitat in South America, which are currently beyond reach. Such a range expansion from climate change has happened, for example, for mountain pine beetles in British Columbia, Canada (Carroll, Taylor, Régnière, & Safranyik, 2003). Future research should consider how simultaneous changes in precipitation and temperature in the Neotropics can alter the constraints on keystone species such as this damselfly.

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SUPPORTING INFORMATION

Additional Supporting Information may be found online in the supporting information tab for this article.

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