Insect Conservation and Diversity

Insect Conservation and Diversity (2019) **12,** 427–436 doi: 10.1111/icad.12354

Predicting hybridisation as a consequence of climate change in damselflies

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Abstract. 1. Climate change is a key stressor for species. Two major consequences of climate-induced range shifts are the formation of new areas of geographic overlap (i.e. sympatry) and an increased probability of hybridisation in the *de novo* created contact zones.

2. One method to effectively quantify the potential of hybridisation is to integrate ecological niche modelling and the propensity to hybridisation based on genetic divergence. In this paper, we have applied this methodology to predict hybridisation outcomes following different scenarios of climate change in 30 species of *Argia* damselflies.

3. We (i) investigated how climate change may affect species' distributions; (ii) quantified if changed distributions generate new areas of sympatry between species; (iii) calculated the propensity to hybridise based on genetic divergence between species; and (iv) integrated these data to predict the future potential of species to hybridise.

4. We found that the distribution of 29 of the 30 species was affected by a change in climate which led to a general increase in sympatric overlap among species. The degree of genetic divergence among the 108 species' combinations ranged from 0.06% to 0.36%. Based on the sympatric overlap and genetic divergence, it can be predicted that 97 of the species pairs are likely to hybridise in the future.

5. Our results are useful to forecast how highly diverse and closely related groups, such as *Argia* damselflies, may respond to a change in climate and how this can impact the potential of species mixing under a scenario of increased global warming.

Key words. *Argia*, climate change, damselflies, ecological niche, genetic divergence, hybridisation, sympatry.

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Introduction

Climate change causes significant stress for the majority of species. For example, an increase in ambient temperature can have significant impacts on the fitness, life cycle, and distribution of species (Parmesan *et al.*, 1999; Hickling *et al.*, 2005, 2006; Sánchez-Guillen & Ott,, 2018), particularly in ectothermic insects (May, 1979). Organisms can respond to such stress in three ways: (i) through short-term, phenotypically plastic (often physiological) adjustments; (ii) by adapting their life history through a more long-term evolutionary response; or (iii) by moving to another geographic area to escape unsuitable areas. The latter response can create novel areas of geographic overlap between formerly allopatric taxa and can also further increase niche overlap between contemporary sympatric taxa (Taylor *et al.*, 2006; Garroway *et al.*, 2010; Sánchez-Guillén *et al.*, 2013, 2016).

In areas of *de novo* sympatry, the potential for interspecific interactions increases, and when these interactions occur between closely related species, this process can lead to hybridisation. Indeed, an increasing number of climate-induced range shifts have now been associated with hybridisation (Kelly *et al.*, 2010; Crispo *et al.*, 2011; Mallet *et al.*, 2011; Abbott *et al.*, 2013). An invertebrate example includes the brown *Argus* butterflies *Polyommatus agestis* and *P. artaxerxes*, which have been shifting northwards in the England and are undergoing frequent species mixing via introgression (Mallet *et al.*, 2011). Another invertebrate examples comes from *Ischnura elegans* and *I. graellsii* damselflies, where *I. graellsii* is mixing with *I. elegans* individuals that have recently established new populations in Spain (Sánchez-Guillén *et al.*, 2011; Wellenreuther *et al.*, 2018). In both cases, the rapid species turnover in the sympatric regions may lead to the future loss of one of the parental species.

The evolutionary consequences of hybridisation can range from local adaptation, and speciation to extinction (Presgraves, 2002; Hoffmann & Sgro, 2011; Sánchez-Guillén *et al.*, 2016). Thus, predicting which species are vulnerable to hybridisation and identifying the geographic areas where this is most likely to happen are of utmost relevance. One way to forecast the likelihood of hybridisation can be achieved by combining Ecological Niche Models (ENM), with the propensity to hybridise based on data on the genetic divergence between species. ENM are useful analytical tools to project the suitable habitat of a species under different climatic scenarios to evaluate range contractions, expansions and to identify areas of species persistence (Peterson *et al.*, 2011). Recently, ENM have been applied to gain insights into a number of different hybridisation scenarios in a diversity of species groups (Sánchez-Guillén *et al.*, 2013; Bariotakis *et al.*, 2016; Otis *et al.*, 2017). In combination with knowledge about the genetic divergence between species, ENM can be used to predict species combinations that are prone to hybridise when forming a secondary contact zone (Sánchez-Guillén *et al.*, 2013). Indeed, studies that estimate hybridisation risk in relation to genetic divergence have now been conducted on a diverse set of species, including birds, amphibians, plants, and insects (Sasa *et al.*, 1998: frogs; Price & Bouvier, 2002: birds; Scopece *et al.*, 2007: orchids; Presgraves, 2002: butterflies; and Sánchez-Guillén *et al.*, 2014: odonates).

Here, we investigate the evolutionary consequences of climate-induced range shifts in 30 species of *Argia* damselflies (Odonata: dragonflies and damselflies). In particular, we determine (i) the extent of current niche overlap and range shifts in response to future climate warming scenarios using ENM projections, with a particular emphasis to understand the increase or creation of novel areas of sympatry between formerly allopatric species; and (ii) the likelihood of species hybridisation in these sympatric areas following these range shifts, using genetic distance as a proxy for predicting the likelihood of species mixing. Among Odonata, the genus *Argia* is a good exemplar group to understand the propensity of hybridisation following an increase in temperature for several reasons. First, it is the most speciose genus within Odonata with more than 126 described species (Schorr & Paulson, 2016; Garrison & Von Ellenrieder, 2017). Second, species are widely distributed and for many an abundance of distributional data is available via data repositories, something which is mandatory for constructing ENM (e.g. Nava-Bolaños *et al.*, 2016). Third, molecular information is available for many *Argia* species (Caesar & Wenzel, 2009; Torres-Pachón *et al.*, 2017), making it possible to calculate the genetic likelihood of hybridisation between species pairs (Sánchez-Guillén *et al.*, 2014).

Material and methods

Species distributional data

Distribution of 30 *Argia* species was compiled based on records from databases (data origin: 66% from http://www.odonatacentral.org, 8% from www.conabio.gob.mx, and 20% from www.gbif.org) and the literature (data origin: 6% from data publications and thesis dissertations). All data were checked carefully for geographic accuracy by removing inconsistent points by eye, for example data inconsistent with the known distribution of species, duplicate information, and references that located species in the sea. Niche models were built only when more than 10 records per species were available. The cleaned data set included 7560 unique presence data points of 30 species (see Table 1) collected over the years 1975–2015. Although these records span the last 40 years, most data were derived from the last 15 years.

Ecological niche models

Study area and environmental predictors. Our study area included North and Central America between the latitudes 53.00 to 0.00N, and longitudes −130.00 to −55.00W. We downloaded WorldClim 1.4 (www.worldc

Table 1. Modelled *Argia* species, their record number, values of validation from True Skills Statistics (TSS), current potential distribution in km^2, and percentage of change in distribution with respect to the current area using RCP 4.5 and 8.5, to 2050 and 2070 years

Species	Records	TSS	Current area (km^2)	Change in future area (%) 2050 RCP4.5	2050 RCP8.5	2070 RCP4.5	2070 RCP8.5
A. alberta	167	0.75	2 486 397	21	26	23	32
A. anceps	71	0.89	358 411	13	19	21	29
A. apicalis	1812	0.74	2 784 061	36	45	41	65
A. cuprea	39	0.90	90 342	−41	−49	−48	−48
A. emma	185	0.77	2 063 013	−15	−25	−22	−41
A. extranea	114	0.88	388 995	−3	−5	0	0
A. funcki	16	0.85	130 143	−9	−10	−7	−20
A. garrisoni	25	0.85	9991	30	103	111	151
A. harknessi	29	0.89	73 428	17	48	39	60
A. hinei	42	0.84	915 571	−2	−4	−7	−12
A. immunda	255	0.85	893 551	69	84	70	92
A. lacrimans	114	0.84	1 262 049	−7	−7	−7	−20
A. leonorae	31	0.88	241 601	−2	−32	−29	−56
A. lugens	11	0.76	1 040 572	−3	−7	−7	−14
A. munda	23	0.89	161 815	55	92	79	139
A. nahuana	261	0.83	1 342 356	51	67	65	105
A. oculata	86	0.88	276 273	16	23	27	36
A. oenea	112	0.88	488 947	19	33	34	62
A. pallens	46	0.87	533 878	43	59	57	78
A. plana	437	0.86	859 630	88	104	92	145
A. pulla	119	0.88	310 682	29	42	31	61
A. rhoadsi	57	0.89	194 479	56	51	47	70
A. sedula	1080	0.76	2 499 501	23	22	23	33
A. tarascana	38	0.87	220 928	12	20	17	21
A. tezpi	78	0.88	198 298	21	33	30	40
A. tibialis	1208	0.80	1 936 853	23	31	23	40
A. tonto	19	0.87	179 823	1	2	5	−9
A. translata	759	0.80	1 801 334	33	27	29	27
A. ulmeca	58	0.89	173 649	26	32	34	60
A. vivida	268	0.77	2 224 638	−9	−18	−15	−34

lim.org) bioclimatic variables for this area (Hijmans *et al*., 2005) using a cell size of 0.041666669. To establish a set of uncorrelated climatic variables, we intersected all variables with 10,000 points randomly placed in the extension of the study area (M). We removed correlated variables with a $r > 0.7$. Thus, the final data set included six uncorrelated variables: mean diurnal range (bio 02), temperature seasonality (bio 04), mean temperature of warmest quarter (bio 10), precipitation of wettest month (bio 13), precipitation of driest month (bio 14), and precipitation seasonality (bio 15).

Background niche selection. To choose the best niche background for each species, preliminary species distribution models were generated with Maxent 3.3.3k (Phillips *et al*., 2006). The following modelling criteria were used to identify the best background: (i) random model: 10 000 data points randomly selected in the study area; (ii) target group model: points taken from the localities of sister species; and (iii) adjusted model to specific area: 1000 data points selected in an area for each species (M), delineated using ecoregions (World Wildlife Fund; www.worldwildlife.org/), and biogeographical provinces (CONABIO; www.conabio.gob.mx). Models were run using default settings ('Auto features', convergence = 10–5, maximum number of iterations = 500) with the exception of the random seed number, which was set to a 30 test percentage setting, and we used 10 bootstrap replicates. We also removed duplicate records and selected the no extrapolation and no clamping option (e.g. regions of environmental space outside the limits encountered during training). The models were evaluated based on the highest area under the curve value (AUC) while minimising the number of model parameters, as well as producing 'closed', bell-shaped response curves guaranteeing model calibration (Elith *et al*., 2010). Based on these comparisons, the model with the best background niche selection was the random model.

Training data sets. Final models were built with the BIOMOD (Biodiversity Modelling) package in R (R Development Core Team, 2008). This package is a platform for predicting species' distributional ranges, including the ability to model the distribution by combining a number of algorithms and test statistics for validation (Thuiller *et al*., 2009). We trained models using four widely used algorithms: Maximum Entropy, Random Forest, Generalized Boosting Methods, and Multivariate Adaptive Regression Splines. These models have all previously been shown to perform well in terms of predictive power (Pliscoff & Fuentes-Castillo, 2011; Reiss *et al*., 2011; Broennimann *et al*., 2012). From individual models obtained with these different algorithms, we generated a 'consensus model'. Such model combinations are the best logistic compromise to avoid both overfitting and overprediction (Merow *et al*., 2014). A total of 70% of the data was used for training the model, and 30% was retained for model validation, with 10 replicate runs. The final model validation was performed using True Skills Statistics (TSS), which denotes the average net rate of successful presence and absence predictions (Liu *et al*., 2009), ranging from −1 to 1, where positive values indicate a higher degree of accuracy and discrimination of the model (Allouche *et al*., 2006) (Table 1). Note that results of these models are not the area in absolute terms that a species occupies, as they do not incorporate population dynamics, a species' dispersal ability, or interactions with other species and human impacts. However, these models can identify areas that contain suitable habitat for a species based on the environmental conditions. This is based on the assumption that the known distribution of species provides sufficient information to characterise its environmental requirements.

A total of 240 models were generated, and model performance was assessed using AUC and TSS statistics, while minimising the number of model parameters. A conservative 10 percentile training presence threshold was used, accepting that a 10% of our presences could be problematic (for a similar rationale, see Sánchez-Guillén *et al*., 2014). The best species models for current climatic conditions were used to generate projections.

Potential future projections

The data for future projections included the following: the most recent data from Global Climate Models (CNRM-CM5, HadGEM2-ES, and MPI-ESM-LR) from the WorldClim database (http://worldclim.org/CMIP5v1). These climate projections were used in the Fifth Assessment (CMIP5) (http://cmip-pcmdi.llnl.gov/cmip5/) report of the Intergovernmental Panel on Climate Change (IPPC) (http://www.ipcc.ch/), and the RCP values (representative concentration pathways which are greenhouse gas concentration trajectories) used were RCP4.5 and RCP8.5 to 2050 and 2070 years.

We calculated the percentage loss/gain of geographic areas in comparison to the current distributions for each species under the two future projection scenarios (i.e. RCP 4.5 and 8.5). For each year we only used the consensus area predicted by all models to calculate the species distribution (Table 1). The potential hybrid zones between each pair of species (for current and future potential distributions) were estimated as the proportion of range overlap between two species. We estimated the overlap areas in km^2 (see Table S1) with the function stringr and raster packages in R.

Genetic divergence and predicted hybrid zones

A phylogeny of the North American *Argia* species, including our 30 study species, was published by Caesar and Wenzel (2009) using one mtDNA gene (16S), and by Torres-Pachón *et al*. (2017) using two mtDNA genes: 16S and cytochrome oxidase subunit I (COI). We downloaded the 16S sequences from GenBank (www.ncbi.nlm.nih.gov/Genbank/) whereas the COI sequences were provided by authors of the two studies (Caesar & Wenzel, 2009 and Torres-Pachón *et al*., 2017). Sequences were aligned with the BioEdit software and pairwise genetic distances were estimated in MEGA v.7 (Kumar *et al*., 2016). The best evolutionary models for genetic divergence were inferred with the JModel test software. For 16S (N = 14 sequences) the best nucleotide substitution model (based on the lowest Bayesian Information Criterion Scores) was the 'Tamura 3-parameter' model (Tamura *et al*., 2011), with a discrete gamma distribution. The 'Tamura 3-parameter' model considers differences between transitions and transversions and provides equal substitution rates among sites. For COI (N = 25 sequences), the best nucleotide substitution model was Tamura-Nei (Nei & Kumar, 2000).

To identify which pairs of species are prone to hybridise, we used a previously estimated genetic divergence threshold for damselflies (see Sánchez-Guillén *et al*., 2014). In this previous study, Sánchez-Guillén *et al*. (2014) found a positive and strong correlation between reproductive isolation and genetic distance for one mitochondrial and one nuclear gene, and estimated that the threshold of genetic divergence was 0.0067 ± 0.011 (range −0.43% to 1.78%) for COII. This meant that species pairs with a genetic divergence value below this threshold would be susceptible to hybridise. Therefore, in our study, we used the threshold of 1.78% of genetic divergence derived from COII to predict putative hybridisation between species because COII is a mitochondrial gene akin to COI and 16S. In insects, these three genes all show a moderate level of evolutionary divergence, although in insects COI is more conserved than COII and 16S (Liu, 1993). To accommodate potential differences in evolutionary rates of COI and 16S compared to COII, we used range thresholds of 1.4–2.2% to ascertain how changing the threshold could alter the estimates for hybridisation.

Results

Current and future potential distributions: predicting sympatric overlap between species

Our models predicted a wide variation in geographic ranges among species. Some species were predicted to occupy fairly small areas (i.e. <20 000 km^2, *A. cuprea*, *A. funcki*, *A. garrisoni*, *A. harknessi* and *A. munda*) whereas others were predicted to occupy large geographic areas (i.e. over 1 million km^2, *A. alberta*, *A. apicalis*, *A. emma*, *A. lacrimans*, *A. lugens*, *A. nahuana*, *A. sedula*, *A. tarascana*, *A. tibialis*, and *A. vivida*) (see Table 1). The relative change in the area predicted by the distribution models projected to RCP 4.5 and 8.5 for 2050 and 2070, respectively, are shown in Table 1. From these data, a clear general trend emerges, namely that the majority of species will experience an increase in their distributional area. For RCP 8.5 and 2070, only *A. extranea* is predicted to remain in the same geographic area as it inhabits now. However, for RCP 8.5 and 2070, nine species are forecasted to decrease the area that they can occupy by 9–56%. Nevertheless, 20 species are predicted to significantly increase the area they can occupy by 21–151%. Similar changes were projected for RCP4.5 and 2070, where just one species (*A. extranea*) is likely to remain in the same geographic area, while 21 species are predicted to increase their area and only eight species are expected to experience a decrease. Notice the case for *A. tonto* which, according to the RCP 8.5 scenario, projected a 9% decrease in distribution, yet a gain of 5% according to the RCP4.5 scenario. Apart from this particular case, directions of change for future distribution models for both scenarios (RCP 4.5 and RCP 8.5) and periods (2050 and 2070) were similar for most *Argia* species (Table 1).

According to contemporary climatic conditions, 125 *Argia* species combinations show allopatric distributions, while 310 species combinations show sympatric distribution (see Table S1 which includes overlapping areas in km^2, and relative species' overlap estimates; Figs 1 and 2a). The range of overlap for each species combination is predicted to increase for both climate change scenarios for 2050 and 2070. The relative change in sympatric areas is presented in Table S1. We found that for 2050 there will be 13 new *Argia* species combinations and a total increase in overlap area of 27.89% (Table S1). In general, these new interactions will be maintained until 2070, and also with a RCP of 8.5 (Table S1). Figure 1 shows the potential hybrid zones (i.e. overlapping areas) for current and future scenarios for 2070 (RCP of 8.5) for all pairwise *Argia* species combinations.

Our RCP 8.5 climate change model indicated the following: 48 out of the 97 species pairs are likely to hybridise based on the close genetic distance and overlap area. Species overlap will increase by more than 10% in the future, while 37 species pairs will decrease future sympatric area of overlap (with more than 10% of area loss) and only 12 will maintain their distribution with <10% of spatial change. Similar changes were found for other projections of climate change (Table S1 and examples in Fig. 3).

Genetic divergence and degree of sympatry

Based on the available sequences, we estimated 153 pairwise genetic distances for COI and 28 pairwise genetic distances for 16S (out of the 436 species combinations). Pairwise genetic distances ranged from: 0.06% (i.e. *A. apicallis* and *A. tezpi*) to 15.72% (i.e. *A. anceps* and *A. tezpi*; Table S1, Fig. 2) for COI; and from 0.03% (i.e. *A. cuprea* and *A. oenea*) and 0.11% (i.e. *A. pulla* and *A. tezpi*) for 16S. For COI, 108 pairwise genetic distances were below the hybridisation threshold obtained from COII (1.78%), and likewise, all16S pairwise genetic distances (28) were below the hybridisation threshold obtained from COII (see Table S1 and Fig. 2b). Using information from both genes (COI and 16S) a total of 115 pairs were found to be prone to hybridise. Furthermore, the range of threshold distances tested (1.4–2.2%) did not change the number of species that were predicted to hybridise. Indeed, our results indicate that species pairs likely to hybridise fall below a 0.36% divergence threshold (see Table S1).

Ninety-seven pairs of species that were found to be prone to hybridise also showed overlapping distributions (see Table S1, and examples in Fig. 4), of which, 43 pairs will increase their sympatric range by more than 10%, and 32 species will reduce their distributional area by more than 10%.

Discussion

Our modelling showed that climate change may lead 20 of the 30 studied *Argia* species to increase their distributional area and that this will lead to an increase in sympatric overlap with close congeners. Notably, we found that the increase of the sympatric areas may affect 43 species pairs, which all show a high likelihood to hybridise. Our projections indicate that distributional ranges will increase predominantly in northern latitudes, as has been reported in other odonate species in central and northern Europe (Hickling *et al*., 2005; Sánchez-Guillén *et al*., 2005, 2011, 2013). Interestingly, contemporary *Argia* distributions already overlap to a great extent, indicating that these species already largely share ecological niche characteristics. Similarly, other Odonata species have been reported to show high niche overlap, which may lead to frequent interspecific sexual interactions at a local scale (Wellenreuther *et al*., 2012). Reduced niche differences in odonates have been explained by sexual selection rather than ecological niche selection as a driving force in the diversification of odonate radiations (Nava-Bolaños *et al*., 2016; Wellenreuther & Sánchez-Guillén, 2016). In fact, this pattern is common in odonate species which usually show large differences in secondary sexual traits, but have small interspecific niche differences (Wellenreuther *et al*., 2012), allowing them to act as ecological equivalents.

Hybridisation rates are generally affected by the extent of species overlap, because overlap is a proxy for encounter rates, and hybridisation rates are particularly expected to be heightened when species are closely related. We detected 115 species pairs with lower genetic divergence than the threshold for hybridisation, indicating that these species may be prone to admixture. Our genetic distance cut-off is a conservative measure to identify pairs of

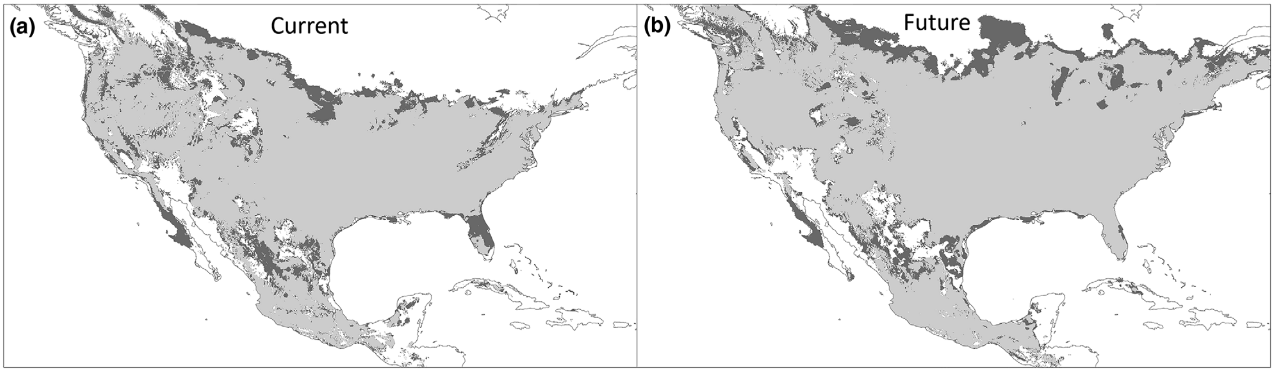

Fig. 1. Current potential sympatric (light grey) and allopatric (dark grey) areas among *Argia* species (a); and future potential sympatric (light grey) and allopatric (dark grey) areas among *Argia* species (b).

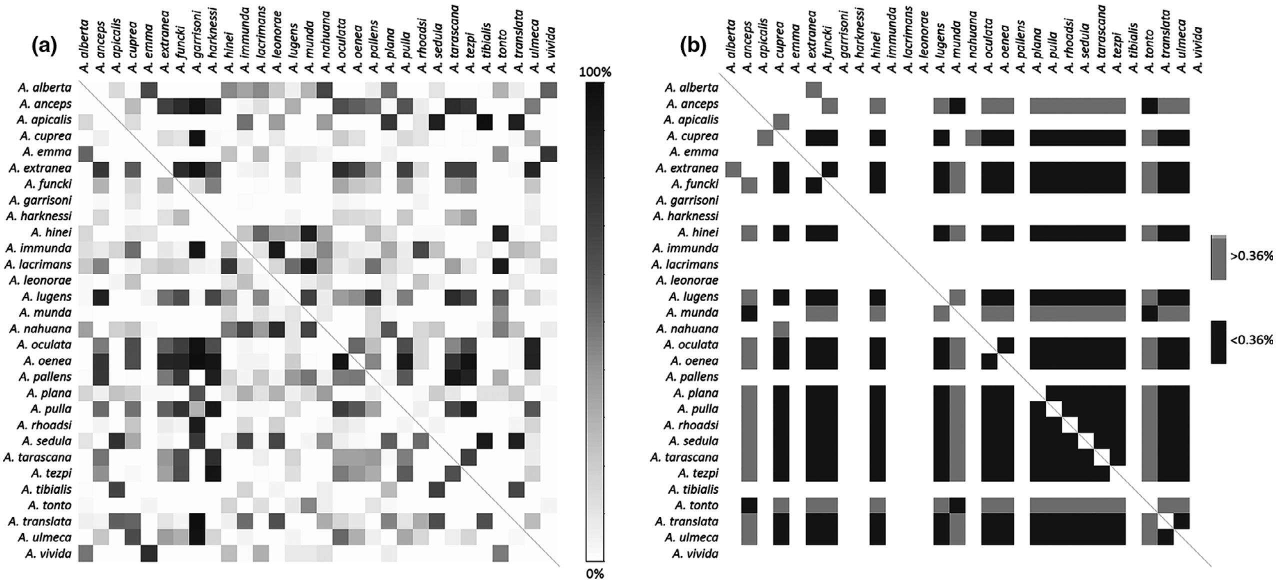

Fig. 2. Matrices of percentage of overlapping area in (a), and genetic distance in (b), between species of *Argia* genus. (a) Percentage of overlapped areas of a particular species with respect to the full area of each corresponding species. In the lower triangular matrix section, the full area reference is corresponding to the species listed on the left, and in the upper triangular matrix section the full area reference is corresponding to the species listed above. (b) An illustration of relative genetic distance for COI between species pairs. Pairs with lower than 0.36% distance are in black squares while species with higher than 0.36% distance are in grey squares.

species that are likely to hybridise once in contact (see Table S1, species in bold letters). Our prediction indicates that 97 of these species pairs are at real risk of undergoing species mixing because they may also share a common geographic space. The potential scenario of hybridisation is especially relevant in the case of *Argia* species because they have recently diversified and thus many pairs exhibit a low genetic divergence. Moreover, as a consequence of their recent diversification, this group also shows a high niche similarity.

Spatial overlap can promote the formation of hybrid zones, and such hybrid zones have been predicted to increase due to climate change on a global level (Sánchez-Guillén *et al.*, 2016). Furthermore, climate change may make some of the current hybrid zones unstable, as seen in some bird species (Engler *et al.*, 2013), where new climatic conditions might induce opposite demographic trends in sympatric populations of each species. Recent studies have shown that odonate hybrids of the genus *Ischnura* can be more successful compared to their parental species (Sánchez-Guillén *et al.*, 2016; Wellenreuther *et al.*, 2018). In these studies, it was found that hybrids displaced parental species from their original habitats through introgressive hybridisation and are adapting to new niches (Wellenreuther *et al.*, 2018). Some outcomes of hybridisation can even include formation of new

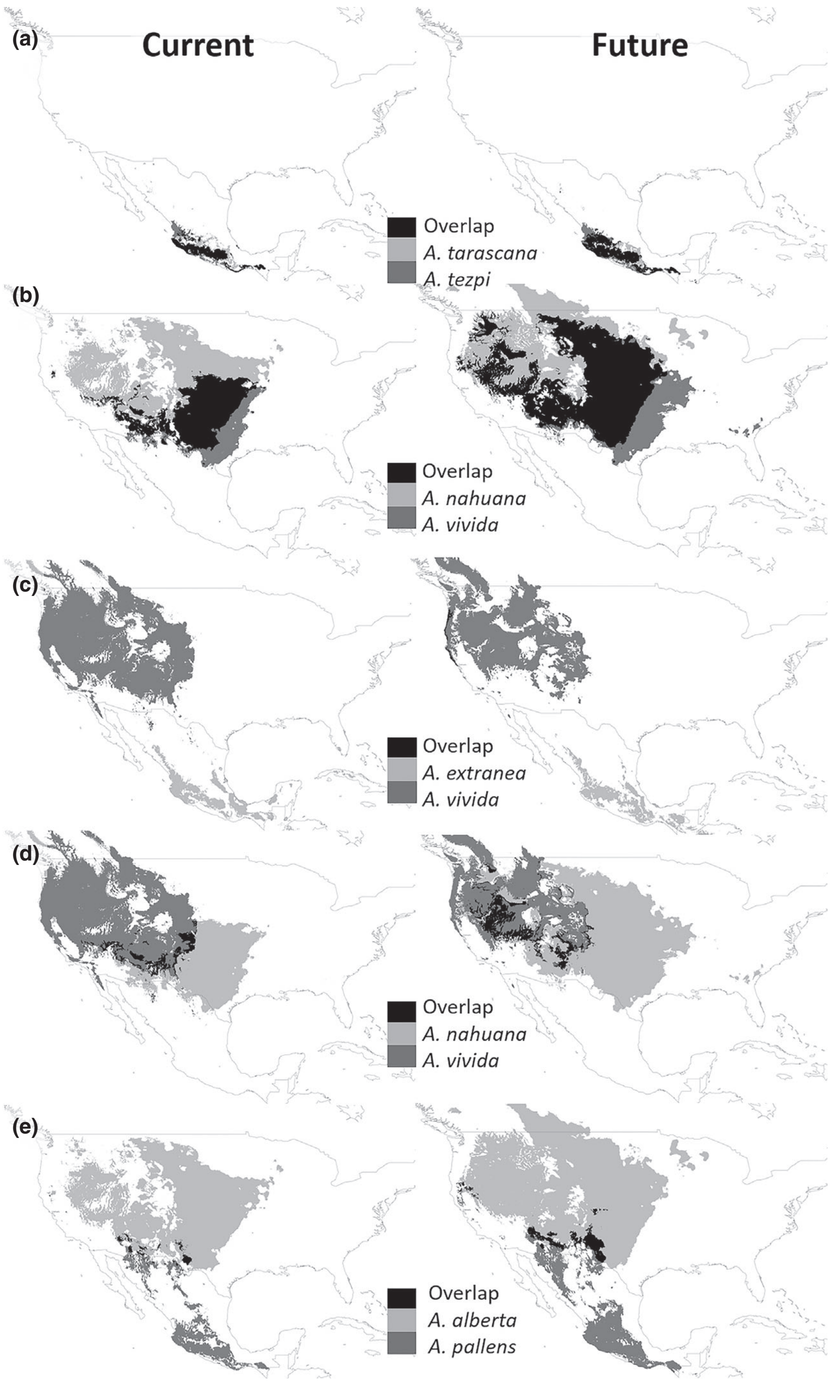

Fig. 3. Selected potential future hybrid (i.e. sympatric) and allopatric (light and dark grey) zones in different *Argia* species pairs. Future was projected for 2070 with RCP8.5. For changes in area of full projections see Table S1.

species, as detected in *Argus* butterflies (Ording *et al.*, 2010; Mallet *et al.*, 2011) and fruit flies (Schwarz *et al.*, 2005). For *Argia* species, the overall low genetic divergence predicts hybridisation between several species' pairs. However, we are unaware if their reproductive isolation patterns can be used to predict which isolation barriers are most porous to undergo species mixing. One exception is that of four sympatric *Argia* species (*A. anceps*, *A. extranea*, *A. oenea*, and *A. tezpi*) where we recently characterised their prezygotic reproductive barriers (Nava-Bolaños *et al.*, 2016). This study indicated that a combination of barriers led to reproductive isolation between all

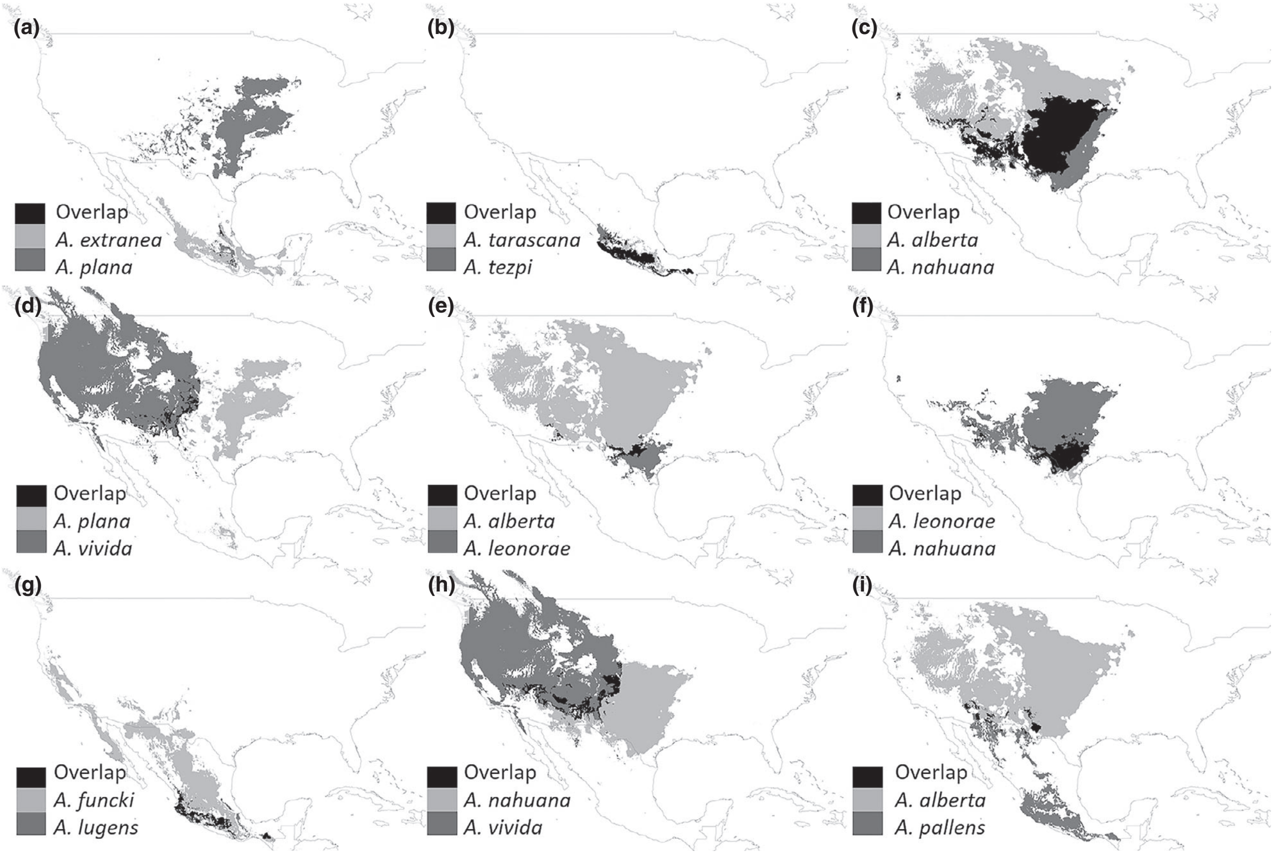

Fig. 4. Selected potential current hybrid (i.e. sympatric) and allopatric (light and dark grey) zones for different *Argia* species pairs.

four species, due to the joint action of visual, mechanical, and tactile isolation (more than 90% of the isolation was due to visual isolation) (Nava-Bolaños *et al*., 2016). This could be explained by the fact the prezygotic barriers could be reinforced in sympatry (Barnard *et al*., 2017; Sánchez-Guillen *et al*., 2011) . Regarding our current predictive model, this suggests that the species combinations between *A. extranea*, *A. oenea*, *and A. tezpi* are likely to produce hybrids based on genetic divergence whereas the three species combinations including *A. anceps* are not prone to hybridise.

Finally, integration of our results with other studies can help to direct conservation efforts to understand and protect odonate biodiversity. For example, two of the species that we identified as species at risk to undergo future hybridisation have already been listed as vulnerable (*A. sabino* and *A. rosseri*) by the International Union of Conservation of Nature's Red List (IUCN, 2018). Conversely, other species not currently cited as at risk may be so according to ENM, like those we present in our present study. This is certainly the case for *A. garrisoni* which has been found to have a relatively small distribution and is sympatric with other closely related *Argia* species (Rangel-Sánchez *et al*., 2018). Another insight that may be gained is that protected natural areas, which were created to enhance biodiversity hot spots, may fail to fulfil this role in the future. Further analyses of how odonate species may expand into these areas in the future or fail to occupy or produce hybrids in these areas will be enlightening. Future research should further investigate these species at risk to see whether their future distribution would indeed lead to hybridisation. In addition, our method can be applied to other vertebrate and invertebrate species to evaluate the evolutionary consequences of hybridisation in response to climate change. Ideally, such further tests can be used to gain insights into to generality of the patterns at a large scale and indicate how species may interact with heterospecifics in the future.

Acknowledgements

Thanks to R. E. Trejo Salazar for the support in genetic analysis between species. To E. Martínez-Meyer, T. P. Feria-Arroyo, and G. Rodríguez-Tapia for their help in niche topics, and to L. A. Osorio-Olvera for the support in R language. A. Nava-Bolaños received a studentship grant from the Consejo Nacional de Ciencia y Tecnología (grant no. 294446/225392) toward a PhD degree of the Programa de Doctorado en Ciencias Biomédicas of the

Universidad Nacional Autónoma de México (UNAM). This paper was financially supported by a PAPIIT UNAM grants IN206618 to AC-A. Authors declare not to have a conflict of interests.

Supporting Information

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

Table S1. Genetic distance and potential hybrid zones among *Argia* species pairs.

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Accepted 11 April 2019

Editor: Christopher Hassall
Associate editor: Nusha Keyghobadi