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Bioclimatic variables derived from remote sensing: assessment and application for species distribution modelling

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Summary

1. Remote sensing techniques offer an opportunity to improve biodiversity modelling and prediction worldwide. Yet, to date, the weather station-based WorldClim data set has been the primary source of temperature and precipitation information used in correlative species distribution models. WorldClim consists of grids interpolated from *in situ* station data recorded primarily from 1960 to 1990. Those data sets suffer from uneven geographic coverage, with many areas of Earth poorly represented.

2. Here, we compare two remote sensing data sources for the purposes of biodiversity prediction: MERRA climate reanalysis data and AMSR-E, a pure remote sensing data source. We use these data to generate novel temperature-based bioclimatic information and to model the distributions of 20 species of vertebrates endemic to four regions of South America: Amazonia, the Atlantic Forest, the Cerrado and Patagonia. We compare the bioclimatic data sets derived from MERRA and AMSR-E information with *in situ* station data and contrast species distribution models based on these two products to models built with WorldClim.

3. Surface temperature estimates provided by MERRA and AMSR-E showed warm temperature biases relative to the *in situ* data fields, but the reliability of these data sets varied in geographic space. Species distribution models derived from the MERRA data performed equally well (in Cerrado, Amazonia and Patagonia) or better (Atlantic Forest) than models built with the WorldClim data. In contrast, the performance of models constructed with the AMSR-E data was similar to (Amazonia, Atlantic Forest, Cerrado) or worse than (Patagonia) that of models built with WorldClim data.

4. Whereas this initial comparison assessed only temperature fields, efforts to estimate precipitation from remote sensing information hold great promise; furthermore, other environmental data sets with higher spatial and temporal fidelity may improve upon these results.

Key-words: AMSR-E, ecological niche modelling, MERRA, remote sensing, South America, species distribution modelling, WorldClim

Introduction

Recent advances in bioinformatics and GIS technologies have greatly facilitated the use of correlative, climate-based models of species niches and distributions in biodiversity analyses (Graham *et al*. 2004; Elith *et al*. 2006; Guralnick, Hill & Lane 2007; Anderson 2012). As a result, a large number of studies now employ climate data to examine and predict the areas suitable for (and potentially occupied by) species across multiple spatial and temporal scales (Carstens & Richards 2007; Waltari *et al*. 2007; Carnaval *et al*. 2009; Nogués-Bravo 2009; Svenning *et al*. 2011). These models primarily rely on a set of highly useful temperature and precipitation grids built from weather station data, the WorldClim data base (Hijmans *et al*. 2005); see also Kriticos *et al*. (2012). WorldClim consists of 19 global gridded data fields created from average monthly temperature and precipitation measurements from weather stations across the world, including data from the Global Historical Climate Network Dataset ver. 3 (GHCN; Lawrimore *et al*. 2011), the World Meteorological Organization climatological data base (WMO 1996) and country-specific weather stations (Hijmans *et al*. 2005). To produce high-resolution grids at up to 30 arc second resolution (roughly 1km), the average monthly measurements were interpolated with elevation as a covariate, using the ANUSPLIN software (Xu & Hutchinson 2011). Bioclimatic variables, reflecting aspects of temperature, precipitation and seasonality thereof, were then derived from the interpolated monthly values. While the

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data have a long temporal range (usually from 1960 to 1990), the spatial coverage provided by the ground station network varies across regions: many arid, boreal and tropical areas have significantly less dense coverage than temperate zones (Hijmans *et al.* 2005).

The field of remote sensing and its utility for climate assessment have also witnessed rapid advancement over recent decades. Satellite remote sensing data sets are becoming increasingly available at high spatial and temporal resolutions and across various portions of the electromagnetic spectrum (e.g. microwave, optical and infrared). In particular, the remote sensing of fields related to conditions at the Earth's surface can support temperature and precipitation measurements and provide a complete synoptic view of contemporaneous and retrospective temperature and precipitation regimes over large areas that otherwise could not be accessed (Adler *et al.* 2000; Justice *et al.* 2002; Jones *et al.* 2010). Remote sensing data from satellite instruments are well suited for the regional-to-global monitoring of surface temperature, providing large areal coverage with high temporal fidelity. Moreover, microwave instruments can operate day and night and are not limited by cloud cover, thus providing the unique capability for acquiring spatially and temporally consistent records of surface temperature and precipitation (Adler *et al.* 2000; Jones *et al.* 2010).

Despite the fact that correlative species distribution models (or ecological niche models; Peterson *et al.* 2011; Anderson 2012) are often developed at regional or continental extents, the number of studies employing remote sensing data is still relatively small; notable exceptions include Bradley & Fleishman (2008), Buermann *et al.* (2008), Saatchi *et al.* (2008), Tuanmu *et al.* (2010, 2011), Bisrat *et al.* (2012) and Papeş, Peterson & Powell (2012). These pioneering studies have used remote sensing data to characterize land cover and vegetation indices, often in combination with WorldClim data, to improve prediction of species ranges (reviews by Gillespie *et al.* 2008; Boyd & Foody 2011; Cord *et al.* 2013). Unlike these studies, we derive bioclimatic variables from remote sensing sources and ask whether and how they lead to models of species distributions different from those built from the widely used station-based WorldClim data. Our ultimate goal is to explore new, alternative ways to improve biodiversity prediction through correlative models.

To do so, we create and explore two bioclimatic data sets from temperature estimates from NASA data sets. The first is derived from the Modern-Era Retrospective Analysis (MERRA, Schubert, Rood & Pfaendtner 1993; Rienecker *et al.* 2011), which incorporates remote sensing information and a subset of the station-based data used in WorldClim within a climate reanalysis framework (the GHCN; Lawrimore *et al.* 2011). The second is based on pure remote sensing information (AMSR-E, Jones *et al.* 2010). The spatial resolution of these data sets is coarse, although the temporal frequency of data collection is high (i.e. near-daily observations at low latitudes). The spatial resolution of MERRA is $1/2 \times 2/3$ degree latitude and longitude (55×75 km), while that of the AMSR-E gridded temperature fields is 25 km (Fig. 1). In some regions, weather stations used to interpolate the WorldClim mean temperature fields are often several times more spatially dense (e.g. in the highly populated Atlantic coast of Brazil and populated coastal and Andean regions of Colombia, Ecuador and Venezuela). However, in areas with sparse weather station coverage (e.g. Amazonia and Patagonia, where stations are on average 200 and 100 km apart, respectively; Fig. 1), bioclimatic variables derived from remote sensing may be more useful in capturing surface field variability relative to WorldClim. Given the coarse resolution of the remote sensing data sets considered herein, we implement a downscaling protocol of the associated bioclimatic data layers. We employ a technique that replicates the downscaling implemented in WorldClim to assess performance of species distribution models at similar spatial scales.

To evaluate the accuracy of these novel experimental global bioclimatic layers, we make two kinds of comparisons. Firstly, as a direct assessment, we compare AMSR-E and MERRA temperature estimates with independently obtained weather station data. Secondly, as an indirect assessment and to explore their contribution to species distribution modelling, we build correlative distribution models for South American vertebrates in four regions with distinct climatic regimes and weather station coverage: the Amazonian and Atlantic forests, the Cerra-

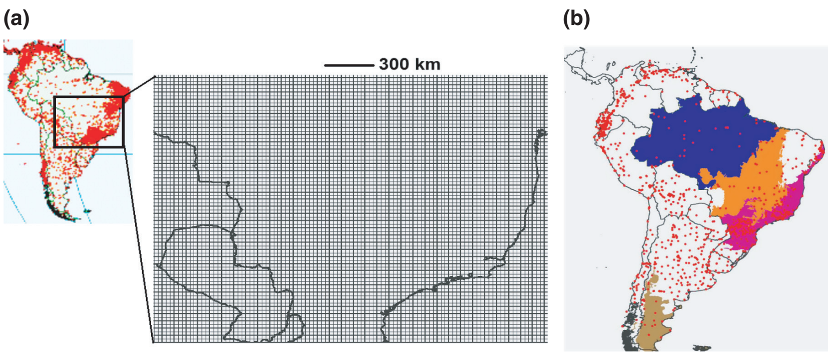

Fig. 1. Maps of South American surface weather stations. Stations a) used to create WorldClim, relative to raster cell sizes of both AMSR-E (inset – smaller pixels) and MERRA (inset – larger pixels, each of which make up six or 2×3 of the smaller pixels) and b) used to compare accuracies of MERRA- and AMSR-E-based mean temperatures, overlaid with the South American regions studied (blue: Amazon; orange: Cerrado; violet: Atlantic Forest; brown: Patagonia).

do and Patagonia (Fig. 1b). Rather than a strict assessment per se, the use of the models should be seen as an exploration of whether the new predictor variables lead to different model outcomes, and furthermore, whether the evaluation statistics indicate that they may be resulting in more informative SDMs given the locality data. Specifically, we compare the accuracy of models built with temperature-based bioclimatic layers derived from WorldClim (based on station data), MERRA (derived via climate reanalysis) and AMSR-E (derived from remote sensing observations), holding the precipitation data constant.

Materials and methods

ASSEMBLY OF MERRA AND AMSR-E DATA SETS

MERRA

The Modern-Era Retrospective Analysis for Research and Applications (MERRA) data set is a weather and climate reanalysis which features the assimilation of modern-era remote sensing data (i.e. the satellite-era from 1979 until present), with a special focus on assimilation of the atmospheric components of the hydrological cycle (e.g. water vapour and precipitation (Rienecker *et al.* 2011). MERRA employs the Goddard Earth Observing System Model version 5 (GEOS-5) Atmospheric General Circulation Model and its atmospheric data assimilation system. The GEOS-5 data assimilation system combines model fields with observations distributed irregularly in space and time into a temporally (1 h) and spatially consistent meteorological grid. Observational input data are utilized from a large array of *in situ* and remote sensing data sets. Along with using a large selection of remote sensing data sets as input, MERRA has an improved spatial and temporal model resolution when compared with other global reanalyses (Rienecker *et al.* 2011).

We utilized time-averaged hourly MERRA single-level temperature at 2 m above the displacement height. From these records, we created monthly maximum and minimum temperatures, which we converted to four bioclimatic temperature fields matching those available through WorldClim. These are mean annual temperature, temperature seasonality (SD $\times$ 100), mean temperature of warmest quarter and mean temperature of coldest quarter. Reanalysis of temperature was provided at the native spatial resolution of MERRA ($1/2 \times 2/3$ degree latitude and longitude, 361×540 grid cells). Using ancillary information on elevation and geopotential height from the Global Land One-km Base Elevation Project (GLOBE) and MERRA, the native resolution temperature fields from MERRA were downscaled to match the 1-km spatial resolution of GLOBE using cubic convolution interpolation, the elevational difference between geopotential height and GLOBE, and the environmental lapse rate for still air (assumed to decrease by 0·6°C per 100 m). We used MERRA data from its inception in 1979 to 2000 to focus on the overlap with the existing WorldClim data set, which employed weather station data primarily from 1960 to 2000. While both MERRA and AMSR-E data sets are global, for the AMSR-E data set (see below) we made grids from tiles F and J from the 1 km GLOBE digital elevation model (DEM), encompassing South and Central America from 13°N to 50°S. All bioclimatic grids generated for this study can be freely downloaded from the Dryad repository [doi:10.5061/dryad.5207q].

AMSR-E

The Advanced Microwave Scanning Radiometer on the Earth Observing System (AMSR-E) supported derivation of daily global land surface temperatures spanning the mission period from 2003 to 2011 (Jones *et al.* 2010). The retrieval of near-daily temperature minima and maxima is obtained by inversion of a simplified semi-physical radiometric model that uses morning and evening brightness temperature observations (Jones *et al.* 2010). The temperature data set provides global temperature retrievals over land for snow and ice-free non-frozen conditions for periods of no precipitation. When compared with the World Meteorological Organization surface station summary and Atmospheric Infrared Sounder and Advanced Microwave Sounding Unit (AIRS/AMSU) surface air temperature retrievals, Jones *et al.* (2010) reported an expected accuracy of 1–3·5°C for the majority of surface stations within vegetated areas, and thus potential biases introduced by vegetation structure that may not be influencing air temperature should be limited to within the accuracy margin.

Descending (morning) and ascending (evening) orbital nodes from AMSR-E's temperature retrieval provide respective minima and maxima for temperature at approximately 2 m height (Jones *et al.* 2010). Hence, we used the temperature observation from the morning and evening satellite overpasses, converted these temperatures to average monthly values, and then derived the same four bioclimatic temperature fields mentioned above. The grid resolution of the AMSR-E temperature fields is approximately 25 km; we downscaled the fields to 1 km using cubic convolution interpolation (Richards & Jia 1998). This downscaling followed that of the MERRA data set, except that the geopotential height (in this case, MERRA topography) was replaced by the 25-km EASE grid GLOBE DEM (Knowles 2001). Data were generated from the 2003–2010 AMSR-E observation period.

GROUND-VALIDATION OF MERRA AND AMSR-E TEMPERATURE FIELDS

We assembled South American surface station data to ground-validate the remote sensing-based temperature fields. For AMSR-E, we used two primary sources: the GHCN (Lawrimore *et al.* 2011) and the WMO climatological data base (WMO 1996). For MERRA, which has input from GHCN weather stations, we avoided biasing conclusions using solely the WMO data base, and also discarding all WMO records from stations located within 50 km of a GHCN-listed station. Using the raw station data, we calculated mean annual temperature (Bioclim 1; Hijmans *et al.* 2005) for each station for comparison with the newly derived MERRA and AMSR-E Bioclim 1 fields. Mean annual temperature was calculated as per Hijmans *et al.* (2005), only including stations with at least 10 full years of data between 1960 and 2000. Because there is no temporal overlap between the AMSR-E data (2003–2010) and WorldClim (1960–2000) or MERRA (1979–2000), we used all weather station data available post-2000 to quantify temperature changes not captured by the latter two data sets. A substantial increase in actual surface temperatures, if detected, would need to be taken into account when comparing the two new data sets.

CORRELATIVE SPECIES DISTRIBUTIONS & MODEL PERFORMANCE

To evaluate the impact of temperature-based bioclimatic variables estimated from WorldClim, MERRA and AMSR-E, we created and compared three sets of species distribution models per species, each differing only in the source of the temperature fields used (mean annual temperature, temperature seasonality, mean temperature of warmest quarter, mean temperature of coldest quarter). The first set employed WorldClim temperature fields, the second used the same four fields derived from the MERRA data set and third set employed the same fields, but derived from AMSR-E. All models also included four precipitation bioclimatic variables from WorldClim (annual precipitation, precipitation seasonality, precipitation of wettest quarter and precipitation of driest quarter), for consistency. Correlative models were built for 20 South American vertebrates (11 frogs, four lizards and snakes and five mammals), across the four study regions (Table 1). All selected taxa were endemic to a single region to enable a better understanding of the differences among remote sensing data sets in different regions.

Correlative distribution models of each species were produced with Maxent version 3·3·3k (Phillips, Anderson & Schapire 2006; Phillips & Dudík 2008). Species distribution models relate known occurrences of species to data describing landscape-level variation in environmental parameters of importance to species' distributional ecology. Maxent in particular uses only presence records, contrasting them with pseudo-absence/background data from the study area using a maximum entropy algorithm to generate a relative suitability value, rescaled to between 0 and 1. Locality data for amphibians and reptiles were taken from published information (Carnaval *et al.* 2009) and personal field records (M. Rodrigues, A. Carnaval, I. Prates, pers. comm.), while the data for mammals were downloaded from the Arctos museum data base (http://arctos.database.museum). The Arctos data were rigorously gathered: they were collected through field surveys in Patagonia by researchers from the University of New Mexico between 2001 and 2007; all records were identified by specialists according to current taxonomy and a uniform set of diagnostic characters (Pardiñas *et al.* 2011). Overall, the occurrence records ranged from 19 to 182 per species (Table 2; Table S1). To lessen the effects of sampling bias (Reddy & Dávalos 2003; Boria *et al.* 2014), we measured the geographical distance between each pair of records for a given species; when two records were found within 10 km of each other, one was randomly removed; the calculation was then repeated until no such pairs existed. In each region, species distributions were modelled using the following extents (Amazon: 13°N-18°S, 42°W-82°W; Atlantic Forest: 3°S-34°S, 34°W-58°W; Patagonia: 25°S-50°S, 48°W-78°W; Cerrado: 1°S-25°S, 34°W-65°W). The species selected for this exercise likely respond to similar barriers to dispersal. Hence, although not species-specific, these region-specific study regions for background sampling reduce the inclusion of areas where species are absent for non-climatic reasons, likely approximating assumptions of model building and evaluation more closely (Anderson & Raza 2010; Anderson 2013). For each environmental data set (WorldClim, MERRA and AMSR-E), we generated five models per species, each based on a different set of training and testing records (the 'cross-validate' option in Maxent, with $k = 5$ bins and each record assigned to one bin at random; in each iteration, four bins representing 80% of the occurrences were used to train the model; and one bin holding 20% of records was withheld for testing); the outputs of these five replicates were then averaged. For simplicity in this initial comparison among the bioclimatic variables used (WorldClim-, MERRA- or AMRS-E-based), all other Maxent settings (e.g. regularization multiplier, feature classes, maximum number of background points, convergence threshold and maximum number of iterations) were set to default.

To evaluate model performance, we plotted and examined test AUC (the area under the ROC curve) for each species and environmental data set combination. AUCs have been shown inappropriate for cross-species comparisons using presence–pseudoabsence or presence-background data (Lobo, Jiménez-Valverde & Real 2008). Our AUC-based comparisons of alternative models for the same set of species are nonetheless valid because only the environmental sources vary across models for each species; occurrence data, extent, resolution and algorithm were held constant (Peterson *et al.* 2011). To compare the AUC scores of the distinct models built for each species, we considered the variance across the five replicates for a given treatment. Because these replicates are not independent, the variance was estimated through the sum of squares multiplied by $(n-1)/n$, rather than divided by $n-1$ (Efron & Tibshirani 1993; Anderson & Raza 2010; Shcheglovitova & Anderson 2013). To examine whether an environmental data set performed consistently better in a given region, we used our species-specific results to compare each pair of average AUC values (MERRA-based vs. WorldClim-based, MERRA-based vs. AMSR-E-based and WorldClim-based vs. AMSR-E-based) and identify which environmental data set resulted in the best performing models for each species. To evaluate the significance of these latter results, we used a sign test (Sokal & Rohlf 1987) to compare the results across all species in a given region, as well as across the entire data set.

Table 1. Species used in correlative distribution modelling.

Species	Region	Taxonomic Group	# Records
Allobates femoralis	Amazon	Amphibian	132
Ameeriga trivittata	Amazon	Amphibian	89
Anolis punctatus	Amazon	Lizard	182
Chatogekko amazonicus	Amazon	Lizard	49
Hypsiboas calcaratus	Amazon	Amphibian	74
Bothrops jararaca	Atlantic	Snake	88
Hypsiboas albomarginatus	Atlantic	Amphibian	33
Hypsiboas faber	Atlantic	Amphibian	27
Leposoma scincoides	Atlantic	Lizard	19
Proceratophrys boiei	Atlantic	Amphibian	74
Chelemys macronyx	Patagonia	Mammal	19
Eligmodontia morgani	Patagonia	Mammal	33
Eligmodontia typus	Patagonia	Mammal	37
Graomys griseoflavus	Patagonia	Mammal	18
Oligoryzomys longicaudatus	Patagonia	Mammal	29
Barycholos ternetzi	Cerrado	Amphibian	29
Chiasmocleis albopunctata	Cerrado	Amphibian	48
Dendrosophus cruzi	Cerrado	Amphibian	41
Eupemphix nattereri	Cerrado	Amphibian	71
Hypsiboas paranaiba	Cerrado	Amphibian	32

Results

Overall, the MERRA-based data set matches the weather station data more closely than the AMSR-E-based estimates, but both of them show geographical trends in over- or underestimates. Both remote sensing data sets tend to over-estimate temperature ranges in central and southern interior portions of South America (across most of the region between Patagonia and the other target areas; Fig. 2). Notably, the estimates from AMSR-E show a strong overestimate in many areas of the northern Andes. In fewer instances, the MERRA and AMSR-

Table 2. Overall and regional rank comparisons of average AUC scores, using sign tests for every pairwise comparison of bioclimatic data sets for temperature. Significantly different rank comparisons are in bold. Note that for the overall comparison, MERRA outperforms AMSR-E for 14/20 species pairs, almost reaching statistical significance.

	Comparison	Outperforming data set	Species pairs performance comparisons	*P*-value
Overall	WorldClim vs. MERRA	None	MERRA > WorldClim in 12/20 species	0·252
	WorldClim vs. AMSR-E	None	WorldClim > AMSR-E in 13/20 species	0·132
	MERRA vs. AMSR-E	None	MERRA > AMSR-E in 14/20 species	0·058
Amazon	WorldClim vs. MERRA	None	WorldClim > MERRA in 3/5 species	0·5
	WorldClim vs. AMSR-E	None	WorldClim > AMSR-E in 3/5 species	0·5
	MERRA vs. AMSR- E	None	MERRA > AMSR-E in 3/5 species	0·5
Atlantic Forest	**WorldClim vs. MERRA**	**MERRA**	**MERRA > WorldClim in 5/5 species**	**0·031**
	WorldClim vs. AMSR-E	None	WorldClim > AMSR-E in 3/5 species	0·5
	MERRA vs. AMSR-E	None	MERRA > AMSR-E in 4/5 species	0·188
Patagonia	WorldClim vs. MERRA	None	WorldClim > MERRA in 4/5 species	0·188
	WorldClim vs. AMSR-E	**WorldClim**	**WorldClim > AMSR-E in 5/5 species**	**0·031**
	MERRA vs. AMSR- E	None	AMSR-E > MERRA in 3/5 species	0·5
Cerrado	WorldClim vs. MERRA	None	MERRA > WorldClim in 4/5 species	0·188
	WorldClim vs. AMSR-E	None	WorldClim > AMSR-E in 3/5 species	0·5
	MERRA vs. AMSR- E	None	MERRA > AMSR-E in 4/5 species	0·188

E-based data sets suggest colder temperatures relative to the weather station records. The ground-validation of the MERRA-based estimates is particularly encouraging in the central and eastern Amazon, the central Atlantic Forest and Patagonia. Fair correspondence between estimated values based on the AMSR-E data set and the weather station data is observed in Amazonia and Patagonia, but not in the Atlantic Forest. Overall, the warm bias in both data sets cannot be explained by the slight increase in temperatures observed between the 1900s (WorldClim's temporal extent) and the 2000s (AMSR-E's temporal extent; Fig. 2c).

The two novel sets of bioclimatic grids are strikingly different from the WorldClim temperature layers, and from each other (Fig. 3). Temperature differences between MERRA-derived layers and WorldClim are most pronounced in the central and southern interior portion of the continent, where MERRA-derived temperatures are higher than WorldClim estimates. AMSR-E-derived temperature estimates, in turn, are substantially higher than WorldClim values in the Caatinga and most of the Andes. Moreover, the MERRA-based data set suggests higher temperature seasonality relative to WorldClim across much of Amazonia and southern South America, while the AMSR-E-based data set suggests higher seasonality in the Caatinga, Patagonia, the Llanos in northwestern South America and other dry and generally open areas of northeastern Brazil. The AMSR-E-based data also suggest

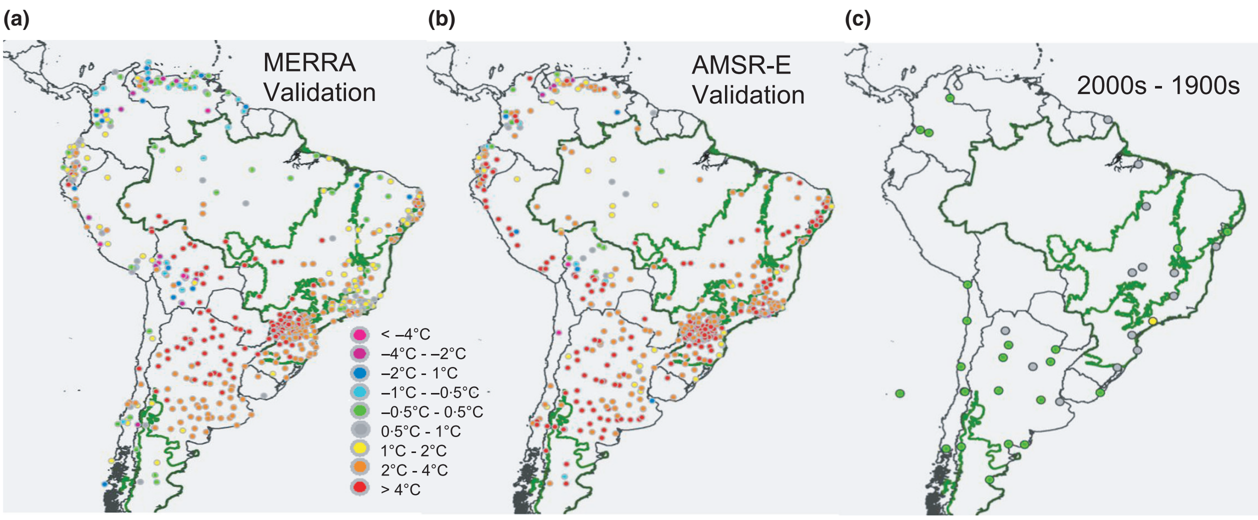

Fig. 2. Ground-validation of MERRA and AMSR-E data relative to mean ground temperatures recorded at 1006 weather stations (years 1950–2000) by the Global Historical Climatology Network and the World Meteorological Organization. Each dot represents a weather station; colours in a) and b) depict the net difference between respective MERRA and AMSR-E estimated temperatures and recorded ground temperature and those in c) indicate the difference in mean temperature recorded at surface weather stations between the more heavily sampled 1950–2000 period and the 2003–2008 period. Green boundaries outline the South American regions examined in the study.

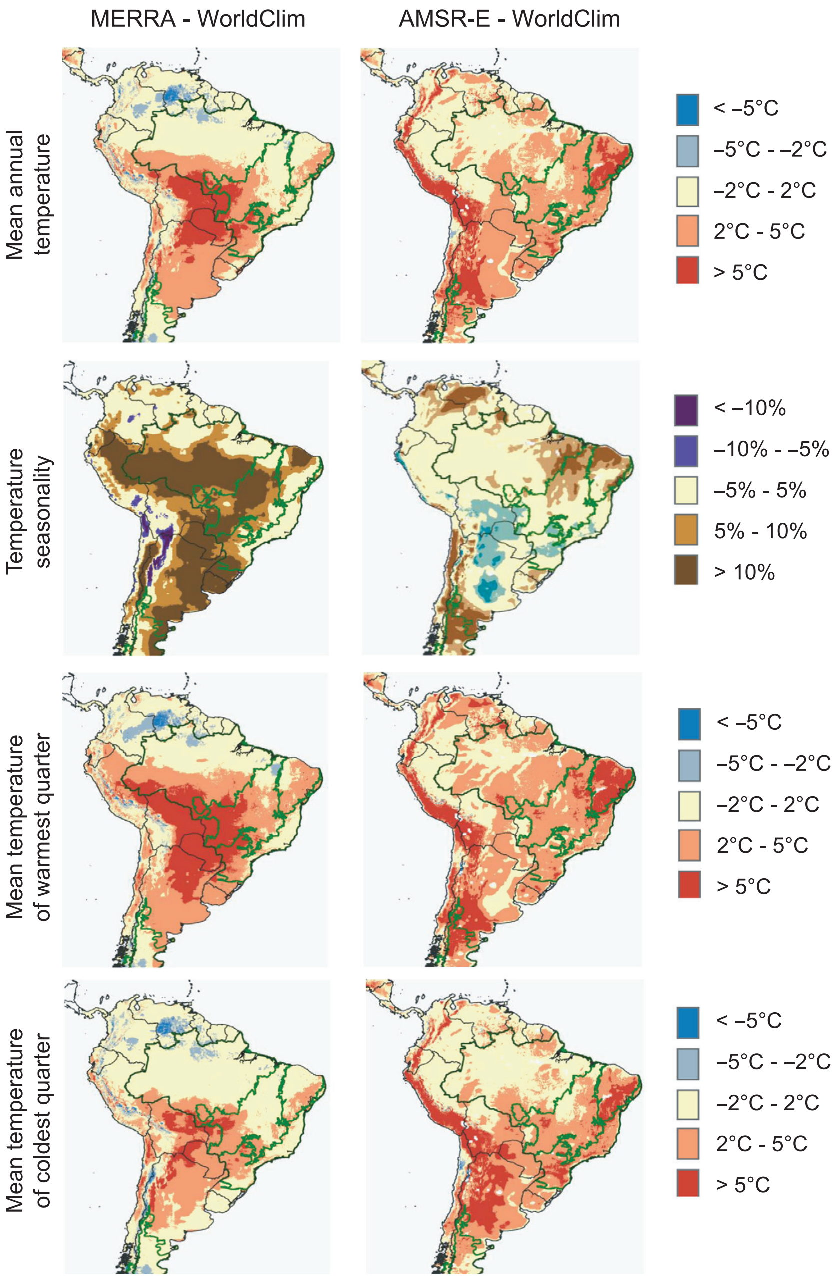

Fig. 3. Differences across values of bioclimatic variables for temperature estimated from MERRA and AMSR-E data sets relative to WorldClim values. Left: difference between MERRA-derived and WorldClim values; right: difference between AMSR-E-derived and WorldClim values. Four bioclimatic variables are illustrated: Bioclim 1 (mean annual temperature), Bioclim 4 (temperature seasonality), Bioclim 10 (mean temperature of warmest quarter) and Bioclim 11 (mean temperature of coldest quarter; Hijmans *et al.* 2005). Values for Bioclim 1, 10 and 11 are given in degrees Celsius, whereas Bioclim 4 values are percentages.

lower seasonality in the interior portion of the continent relative to WorldClim.

Species distribution models made from WorldClim, MERRA and AMSR-E temperature fields differ in performance (e.g. Figs 4, 5; all model output maps are provided in Figs S1–S20). However, the variation in average AUC scores for individual species is always within two corrected standard errors (Fig. 5, Table S2). Regional differences are nonetheless observed: in the Atlantic Forest region, the performance of MERRA-based models is significantly greater than those of WorldClim-based models (Fig. 5, Table 2). In Patagonia, the performance of WorldClim-based models is significantly greater than those of AMSR-E-based models. In Amazonia and the Cerrado, AUC values of WorldClim, MERRA and AMSR-E-based models do not differ significantly. When the results of all species are combined into a single sign test, no significant differences are detected in the performance of models built from MERRA, AMSR-E or WorldClim-based data sets, but the performance for MERRA is nearly significantly higher than that of AMSR-E (Table 2).

Discussion

To test whether newly developed remote sensing data sets can be used in correlative species distribution modelling, we have compared AMSR-E and MERRA temperature estimates with independently obtained weather station data and have built distribution models for South American vertebrates in four regions with distinct climatic regimes and weather station coverage. Validation using data sets from weather stations,

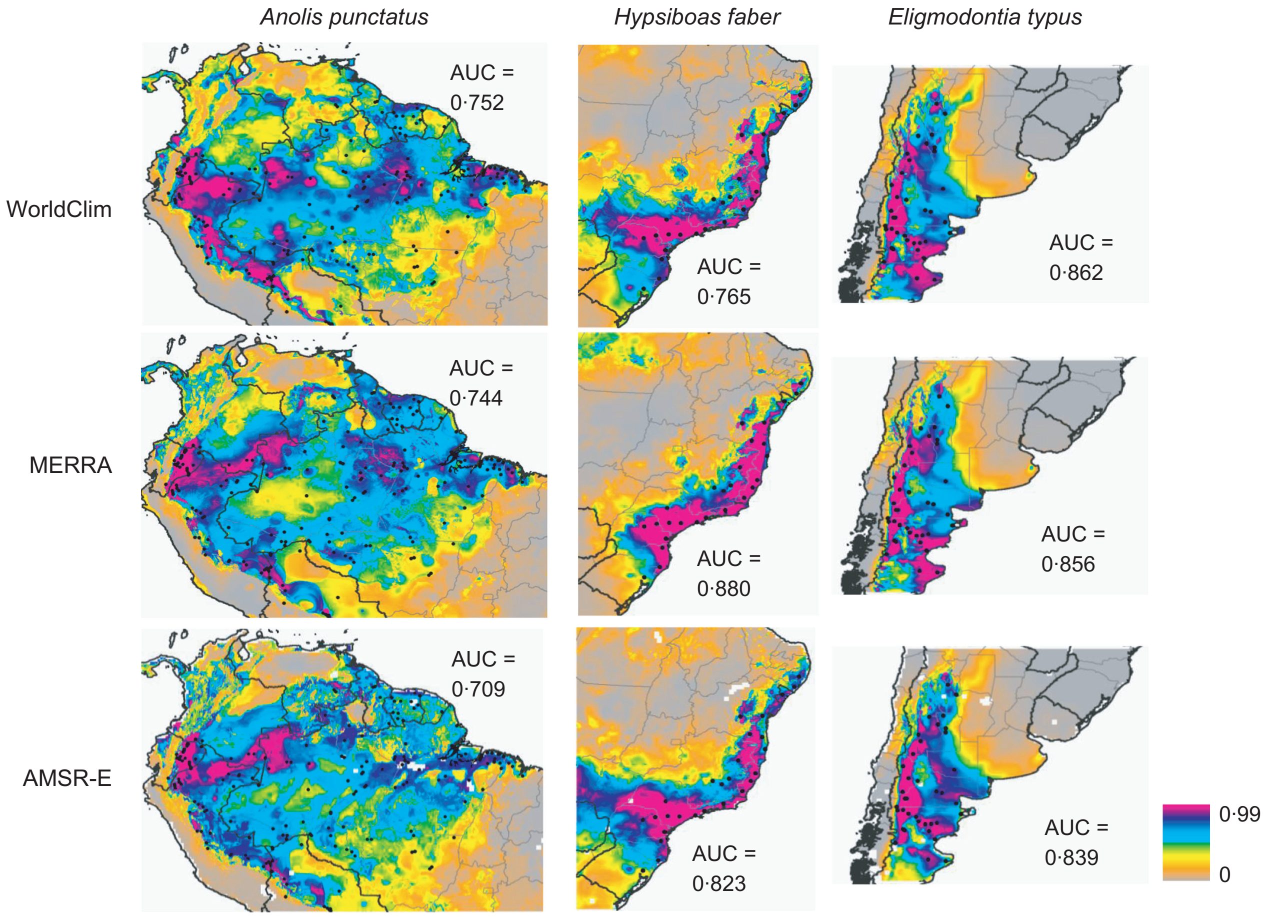

Fig. 4. Selected species distribution models using WorldClim (top panels), MERRA-derived (centre panels) and AMSR-E-derived (bottom panels) bioclimatic variables for temperature and the same grids for precipitation (WorldClim). Examples include models focusing on the Amazon (left, for the lizard *Anolis punctatus*), the Atlantic Forest (middle, for the frog *Hypsiboas faber*) and Patagonia (right, for the mammal *Eligmodontia typus*) using Maxent with logistic output, so that grey through green colours represent less suitable climatic conditions and blue and violet colours represent more suitable ones. Dots indicate occurrences used.

comparisons with WorldClim products and distribution model comparisons consistently show that the relative performance of MERRA- and AMSR-E-derived data sets is region-specific. This is not unexpected: the AMSR-E and MERRA data sets differ in their temporal extent, native spatial resolution, the degree to which data set derivatives reflect surface stations and remote sensing inputs, and the nature of the retrievals. There is an obvious positive bias in temperature estimates derived from MERRA relative to the *in situ* station data and the WorldClim data set throughout most of interior central and southern South America. A previous study documented a general warm and dry bias in the MERRA data set, particularly in low and mid-latitude regions (Yi *et al*. 2011), attributing it to effects of cloudiness and shortwave radiation. In contrast, the AMSR-E data set fails to match weather station data accurately in the Andes and differs substantially from WorldClim estimates in the region – an expected result considering that the AMSR-E temperature retrievals are limited to snow- and ice-free conditions (Jones *et al*. 2010). It is thus not surprising to observe that the AMSR-E-based models were outperformed by WorldClim in the temperate Patagonian region (Fig. 4). Notably, AMSR-E data sets indicated higher estimates of temperature seasonality in dry but periodically wet, open areas in several parts of the continent (e.g. the savannas of the Venezuelan and Colombian Llanos). These temperature patterns are similar to those from Strahler *et al*.'s (1999) MODIS (Moderate-resolution Imaging Spectroradiometer) land cover distribution map, suggesting enhanced temperature sensitivity to land cover effects that are not realistically captured by WorldClim and MERRA.

The results of the MERRA-based analyses were nonetheless encouraging. This data set enabled ground-validated estimates of bioclimatic variables in regions of sparse weather station coverage such as Amazonia and Patagonia. Yet, as the region-based comparisons attest (Table 2), MERRA-based distribution models performed similarly to WorldClim-based models in these areas. This outcome may be a result of the relatively coarse native resolution of the MERRA product and suggests that the interpolation technique used by WorldClim may be sufficient and appropriate to overcome the lack of station information in regions of little topographic complexity (Hijmans *et al*. 2005).

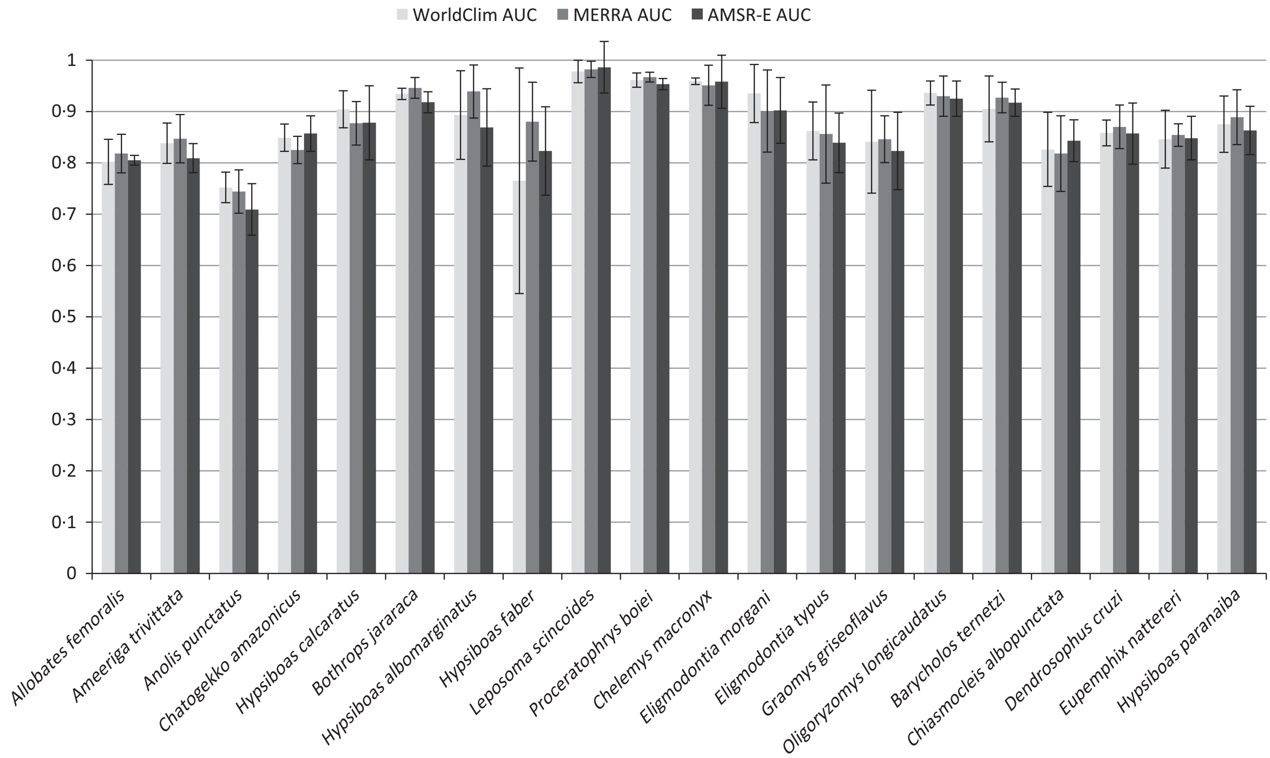

Fig. 5. Species and regional comparisons of average AUC scores. Error bars indicate 1·96 $\times$ the corrected standard error (see text).

The MERRA data set also resulted in overall improved AUCs for the Atlantic Forest, a weather station rich region where WorldClim might be expected to outperform the other environmental data sources. Predicted species distributions for the Atlantic Forest frog *Hypsiboas faber*, for instance, show clear differences depending on the environmental data set utilized (Fig. 4). Specifically, the WorldClim-based model overpredicts the species' occurrence in inland portions of the southern Atlantic Forest and nearby portions of the Cerrado, an error not made by MERRA-based models. We posit that there may be two alternative explanations for this. Because the Atlantic Forest region is highly topographically complex, with mountain ranges and valley systems running parallel to the coast (Morellato & Haddad 2000), perhaps the interpolation schemes used to create the WorldClim data set underestimated real variations in temperature, which were in turn detected by the MERRA climatological re-analysis and lapse rate downscaling. Such fine-grain differences indeed are likely to be detected in the performance of distribution models in this region, given the high spatial density of biological sampling. Alternatively, it is possible that the MERRA-based bioclimatic layers more accurately describe the environmental conditions experienced in the Cerrado and interior Atlantic Forest regions that were incorrectly predicted as suitable by the WorldClim-based models.

While our study focuses solely on temperature data, precipitation will certainly prove useful in future explorations. In 12 of the 20 species studied, the most important variable in the final models turned out to be a precipitation variable, as indicated by model lambda values (Phillips, Anderson & Schapire 2006). Therefore, any improvements over current station-based estimates, afforded using remote sensing data of precipitation, will likely result in greater model improvements. Such precipitation estimates are available from the TRMM (Tropical Rainfall Measuring Mission) data set (Huffman *et al.* 2007) at 4 km resolution, and this data set would be a prime candidate for consideration. Despite being limited to cloud-free regions, and thus problematic in the tropics, MODIS instrument data sets (King *et al.* 2003) also provide measurements at a resolution of 1 km that might be well suited for distribution modelling. It is likely that amalgams of data sets, where distinct data sources are used for different regions, will be needed to best leverage remote sensing data sets; these combined data sources have the best prospects for improving bioclimatic analyses (Turk & Miller 2005).

We also foresee correlative distribution modelling techniques broadening beyond the derivation of commonly used bioclimatic variables, such as the ones explored here, and incorporating novel variables. For example, remote sensing will be invaluable to the characterization of changes in diurnal environmental cycles that may be intimately linked to animal movement and habitat use, or of seasonal changes that drive migratory and dispersal patterns. As with all correlative modelling, these novel bioclimatic layers may not be direct causal drivers of species distributions, but may increase the predictive power of such models and thus generate better hypotheses for future testing. Our initial results indicate that remote sensing measures show promise, but that the amalgamation of multiple remote sensing data sets, the improvement of temporal windows and resolution, and the exploration of other variables from satellite data (e.g. temperature extremes; Ashcroft *et al*. 2014) are all avenues that can lead to more accurate niche description and biodiversity modelling in the very near future.

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Data accessibility

All bioclimatic grids generated for this study can be freely downloaded from the Dryad repository: http://datadryad.org/resource/doi:10.5061/dryad.5207q.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Fig. S1–S20. Distribution models for 20 South American species built with environmental grids from the three different temperature sources (WorldClim, MERRA and AMSR-E) and the same grids for precipitation (WorldClim)

Table S1. Occurrence records used for species distribution modeling.

Table S2. Performance of species distribution models built with environmental grids from the three different temperature sources (WorldClim, MERRA and AMSR-E) and the same grids for precipitation (WorldClim).