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Climatic requirements of the eastern paralysis tick, *Ixodes holocyclus*, with a consideration of its possible geographic range up to 2090

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ABSTRACT

The eastern paralysis tick, *Ixodes holocyclus*, is an ectoparasite of medical and veterinary importance in Australia. The feeding of *I. holocyclus* is associated with an ascending flaccid paralysis which kills many dogs and cats each year, with the development of mammalian meat allergy in some humans, and with the transmission of *Rickettsia australis* (Australian scrub typhus) to humans. Although *I. holocyclus* has been well studied, it is still not known exactly why this tick cannot establish outside of its present geographic distribution. Here, we aim to account for the presence as well as the absence of *I. holocyclus* in regions of Australia. We modelled the climatic requirements of *I. holocyclus* with two methods, CLIMEX, and a new envelope-model approach which we name the 'climatic-range method'. These methods allowed us to account for 93% and 96% of the geographic distribution of *I. holocyclus*, respectively. Our analyses indicated that the geographic range of *I. holocyclus* may not only shift south towards Melbourne, but may also expand in the future, depending on which climate-change scenario comes to pass.

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1. Introduction

The eastern paralysis tick, *Ixodes holocyclus*, and the southern paralysis tick, *Ixodes cornuatus*, are ectoparasites of medical and veterinary importance in Australia and among the 70 or so species of ticks known to cause paralysis as a result of their blood feeding (Durden and Mans, 2016). Among these 70 species of ticks, *I. holocyclus*, the eastern paralysis tick, seems to have the most potent toxin (Barker and Walker, 2014; Durden and Mans, 2016). When *I. holocyclus* feeds, holocyclotoxins, a family of neurotoxins, are injected into the host with the saliva of the tick, which may cause paralysis (Cooper and Spence, 1976; Masina and Broady, 1999; Chand et al., 2016; Karbanowicz et al., 2017; Rodriguez-Valle et al., 2018). Although death due to tick paralysis has long been attributed solely to the paralysis of respiratory muscles, Atwell et al. (2001) argued that death due to tick paralysis can also be caused by cardiopulmonary dysfunction. There are 20 documented human fatalities from *I. holocyclus*; comparable to fatalities from redback spiders (18 deaths) and funnel-web spiders (13 deaths) (Sutherland and Tibballs, 2001; Barker and Walker, 2014). Thank-

fully, human fatalities from the feeding of *I. holocyclus* are now rare since the advent of intensive care units in regional hospitals and advances in medical treatment (Barker and Barker, 2018). Deaths of dogs and cats however, are still very common in Australia, either directly from paralysis or from euthanasia due to complications from tick paralysis (Atwell et al., 2001). Indeed, the case fatality rate of dogs and cats inflicted with tick paralysis may be as high as 17% and 22%, respectively (Eppleston et al., 2013). Apart from paralysis, *I. holocyclus* may cause mammalian meat allergy in humans who have been fed on by ticks (van Nunen et al., 2007, 2009; van Nunen, 2015, 2018). There have been at least 600 cases of mammalian meat allergy caused by *I. holocyclus* along the eastern coast of Australia (van Nunen, 2015). These hyper-immune patients presented with urticaria, angioedema, respiratory distress and syncope approximately 3–6 h after they ate red meat (van Nunen et al., 2009; van Nunen, 2018).

The known geographic distribution of *I. holocyclus* is along most of the eastern coast of Australia, from Shiptons Flat, just north of Cairns in Far North Queensland, to Lakes Entrance in the Shire of East Gippsland, Victoria (Fig. 1A) (Roberts, 1970; Barker and Walker, 2014; Barker and Barker, 2018). Although the geographic distribution of *I. holocyclus* is now very well known (Barker and Barker, 2018), it is not known why *I. holocyclus* is apparently absent

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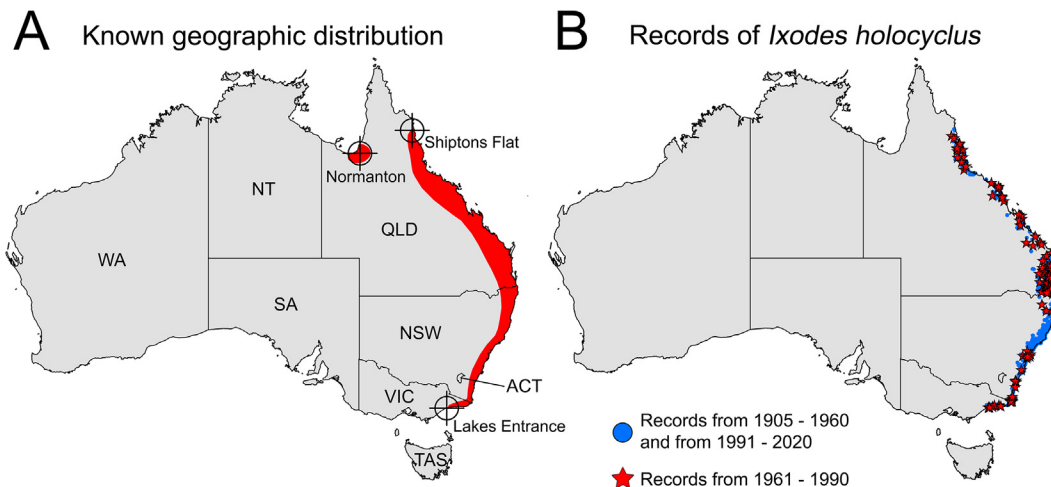


Fig. 1. The geographic distribution of *Ixodes holocyclus*, the eastern paralysis tick. (A) The geographic distribution of *I. holocyclus* since Seddon (1951), adapted from Barker and Walker (2014). (B) The 1804 published occurrences (records) of *Ixodes holocyclus* (Barker and Barker, 2018): the circles indicate the 1667 records from 1905 to 1960 and from 1991 to 2020; and the stars indicate the 137 records of *I. holocyclus* from 1961 to 1990.

from Cape York Peninsula despite a seemingly suitable climate and the presence of suitable hosts (Travouillon, 2016; Warburton and Travouillon, 2016). It is also not known why this tick is enzootic in some regions (i.e. able to persist and thus complete its life-cycle year after year at a location; compared with epizootic, occurring from time to time (*sensu* Barker and Barker 2019) yet absent from other regions, even though these regions are often adjacent to one another. Finally, it is not known why *I. holocyclus* is unable to establish and thus become enzootic in regions south-west of Lakes Entrance such as Melbourne, Victoria, even though *I. holocyclus* is often taken to Melbourne by humans and their domestic animals, especially dogs, from the Shire of East Gippsland where *I. holocyclus* is enzootic, (Beveridge, 1991; Kelers et al., 2012; Barker and Barker, 2018, 2019). Moreover, *I. holocyclus* is considered to be catholic in its feeding habits, since it is known to feed, apparently to repletion, on over 30 different species of animals including humans (Roberts, 1970; Barker and Walker, 2014); although, importantly, it is not known how viable the eggs and the larvae are, from female *I. holocyclus* that have fed on most of these 30 plus species of hosts.

Heath (1974) hypothesised that the geographic distribution of *I. holocyclus* was constrained to either: regions with an annual rainfall of more than 1000 mm; regions that had a saturation deficit of less than 7 mmHg in December; or regions with a Meyer's ratio of more than eight in November. These projections, however, could not be extrapolated accurately to the entire geographic distribution of *I. holocyclus* (Heath A.G.C., 1974. An investigation into temperature and humidity preferenda of ixodid ticks, and their distribution in relation to bioclimatic zones in Australia. PhD thesis. The University of Queensland, Australia).

Here, we aim to account for the geographic distribution of *I. holocyclus* (where the tick has been found i.e. *presence*) with variation in climate. Secondly, we aim to explain why *I. holocyclus* is apparently unable to become enzootic (where the tick has not been found i.e. *absence*) in some regions of Australia despite seemingly suitable climate and hosts (Heath, 1974; Barker and Walker, 2014; Barker and Barker, 2018). These regions are, from north to south, Kutini-Payamu (also known as Iron Range) National Park on Cape York Peninsula in Queensland; Normanton and Dalby in Queensland; and Melbourne in Victoria. Lastly, we project the geographic range (range of suitable habitat) of *I. holocyclus* under various climate-change scenarios.

2. Materials and methods

2.1. Climatic data

Climatic data were downloaded from CliMond (<https://www.climond.org>) (Kriticos et al., 2012) at 10' resolution (10' latitude by 10' longitude; approximately 17.5 km × 18.9 km at the northern-most point of Cape York Peninsula; 13.7 km × 18.9 km at the southern-most point of Tasmania) for both the 1961–1990 average and future (2030, 2050, 2070 and 2090) climate-change scenarios. The climatic data from both the 1961–1990 and future climate-change scenarios consisted of mean daily minimum and maximum temperatures and relative humidity at 09:00 h and 15:00 h by month, and monthly rainfall (Kriticos et al., 2012). For the 1961–1990 dataset, these climatic variables were averaged from 1961 to 1990 (30 years) by month whereas for the future climate-change scenarios, projections for 2030, 2050, 2070 and 2090 were from the Intergovernmental Panel for Climate Change (IPCC) Special Report on Emissions Scenarios (SRES) A1B and A2 climate-change scenarios, from the CSIRO-Mk3 and MIROC-H climate models (Kriticos et al., 2012).

2.2. Data preparation

There were 1804 published occurrences (records) of *I. holocyclus*; these records were accumulated from 1905 to 2020 (Barker and Barker, 2018) (Fig. 1B). However, we studied only the records of *I. holocyclus* from 1961 to 1990 to match the time-period of the climate dataset of Kriticos et al. (2012). Of the 1804 records, 137 records were from 1961 to 1990 (Fig. 1B).

2.3. CLIMEx

CLIMEX (Sutherst and Maywald, 1985; Sutherst et al., 2007; Kriticos et al., 2016) is a species distribution model that uses algorithms to calculate an Ecoclimatic Index (EI), which is scaled from 0 to 100, to measure the climatic-suitability of a location for the modelled plant or animal. EIs are calculated from the Growth and Stress Indices which are measures of the response of plants or animals to climate (Sutherst and Maywald, 1985; Sutherst et al., 2007; Kriticos et al., 2016). In the present study, we classified regions of Australia by their Ecoclimatic Index; 0 indicated that the

climate was unsuitable; 1 to 10 indicated that the climate was marginal; 11 to 20 indicated that the climate at the location was sufficiently suitable to support *I. holocyclus*; and 21 to 100 indicated highly favourable climates for *I. holocyclus* (Sutherst and Maywald, 2005).

Heath (1974) studied the effects of temperature and humidity on the eggs, larvae, nymphs and adult *I. holocyclus* in the laboratory. Heath (1974) found that: the lower temperature threshold of survival for all life stages of *I. holocyclus* was 8 °C to 13 °C; the optimal temperature range for *I. holocyclus* larvae survival was 25 °C to 28 °C; and the upper temperature limit of survival for *I. holocyclus* eggs, larvae and nymphs was approximately 32 °C. We used these temperatures for the CLIMEX parameters, DV0, lower threshold of temperature; DV1, lower limit of optimal temperature; DV2, upper limit of optimal temperature; and DV3, upper threshold of temperature, respectively. We then studied the soil moisture at the locations where *I. holocyclus* had been recorded from 1961 to 1990, and inferred SM0, lower threshold of soil moisture; SM1, lower limit of optimal soil moisture; SM2, upper limit of optimal soil moisture; and SM3, upper limit of soil moisture. Lastly, with the 1961–1990 climate dataset (Kriticos et al., 2012), we fitted, iteratively, the 12 other CLIMEX parameters which relate to cold, dry, heat and wet stress until a best fit to the 137 records of *I. holocyclus* from 1961 to 1990 (Fig. 1B) was obtained (Table 1). The CLIMEX output of EIs were then sorted by their value, after Sutherst and Maywald (2005).

To test our CLIMEX model, we 'spatially joined', with ArcGIS, the 137 records of *I. holocyclus* from 1961 to 1990 to the projected geographic range (regions inferred to be suitable; EI > 0) of *I. holocyclus* from our CLIMEX model. Similarly, we also 'spatially joined' the 1804 records of *I. holocyclus* from Barker and Barker (2018) to the projected geographic range of *I. holocyclus* from our CLIMEX model, to see whether or not our CLIMEX model could also account for the distribution of *I. holocyclus* before 1961 and after 1990.

Table 1
CLIMEX parameters for *Ixodes holocyclus*, the eastern paralysis tick.

Parameter	Mnemonic	Value
1. Moisture index		
Lower threshold of soil moisture	SM0	0.3 ^a
Lower limit of optimal soil moisture	SM1	0.5 ^a
Upper limit of optimal soil moisture	SM2	1.0 ^a
Upper threshold of soil moisture	SM3	1.4 ^a
2. Temperature index		
Lower threshold of temperature (°C)	DV0	9 ^b
Lower limit of optimal temperature (°C)	DV1	25 ^b
Upper limit of optimal temperature (°C)	DV2	28 ^b
Upper threshold of temperature (°C)	DV3	32 ^b
3. Cold stress		
Cold stress temperature threshold (°C)	TTCS	9 ^b
Cold stress temperature rate	THCS	−0.0001 ^c
Cold stress degree-day threshold	DTCS	10 ^c
Cold stress degree-day rate	DHCS	−0.0075 ^c
4. Heat stress		
Heat stress temperature threshold (°C)	TTHS	32 ^b
Heat stress temperature rate	THHS	0.02 ^c
Heat stress degree-day threshold	DTHS	2 ^c
Heat stress degree-day rate	DHHS	0.004 ^c
5. Dry stress		
Dry stress threshold	SMDS	0.3 ^a
Dry stress rate	HDS	−0.07 ^c
6. Wet stress		
Wet stress threshold	SMWS	1.4 ^a
Wet stress rate	HWS	0.002 ^c

^a Parameters inferred from the climate where *I. holocyclus* has been found.

^b Parameters from laboratory experiments of Heath (1974).

^c Parameters fitted iteratively by us.

2.4. Climatic-range method

The climatic-range method (Teo et al., unpublished data), drew from Shelford's Law of Tolerance (Shelford, 1913), which in the context of geographic distributions, can be understood as whether or not a species is able to tolerate climatic conditions and hence become enzootic at a location. The known geographic distribution of a species is thus a representation of the climatic conditions the species can tolerate. We studied the climate at locations where *I. holocyclus* has been found, to learn about the range of climates tolerable to *I. holocyclus* (climatic-profile of *I. holocyclus*) and then used this range of climates to account for the suitability of other locations in Australia. Our climatic variables of interest were minimum and maximum temperature, and Meyer's precipitation to saturation deficit ratio, otherwise known as 'Meyer's N.S. Quotient' or 'Meyer's ratio' (Meyer, A., 1926. Ueber einige zusammenhänge zwischen klima und boden in Europa (in German). PhD thesis. ETH Zurich, Switzerland). Minimum and maximum temperatures inform us about the temperature range that *I. holocyclus* can tolerate whereas Meyer's ratio, which is a measure of the efficiency of rainfall in mitigating dry conditions (Meyer, 1926; Prescott, 1946), seems to be closely related to the moisture balance of arthropods (Key, 1942a, 1942b; Clark, 1953). Moreover, Meyer's ratio is derived from saturation deficit, which has been shown to affect the questing activity and duration of questing of *Ixodes ricinus*, the Lyme disease vector: these ticks were less active in high saturation deficit (drier) conditions, and more active in low saturation deficit (moister) conditions (Randolph and Storey, 1999; Perret et al., 2000, 2003). We note that Heath (1974) showed that the survival of *I. holocyclus* was impacted negatively by high saturation deficits.

We 'spatially joined', with ArcGIS 10.6.1, the 137 records of *I. holocyclus* between 1961 and 1990 from Barker and Barker (2018), to the 10' × 10' grid of Australia. These 137 records fell into 96 of the 10' × 10' grid-squares. The averaged climatic data from 1961–1990 (Kriticos et al., 2012), for the 96, 10' × 10' grid-squares, were then extracted. The average of mean daily minimum and maximum temperatures was regarded as mean temperature whereas the average of the mean daily 09:00 h and 15:00 h relative humidity was regarded as mean relative humidity. The mean daily saturation deficit for the month (Randolph and Storey, 1999) and monthly Meyer's ratio (Meyer, 1926) were calculated with these averages. The highest and lowest values for each climatic variable were then used to infer the range of climates tolerable to *I. holocyclus* (estimated climatic profile).

The climate in all of the 10' × 10' grid-squares of Australia ($n = 25,360$) was then compared with our estimated climatic-profile of *I. holocyclus*. If the climate of a grid-square fell in our estimated climatic-profile of *I. holocyclus* for the month, a value of '1' was given and the grid-square was inferred to be suitable for *I. holocyclus* for that month. To identify grid-squares that may support enzootic populations of *I. holocyclus*, the value for each month for each grid-square was summed from December to March because the larvae are most abundant in the environment from January to March (Doube, 1979; Barker and Walker, 2014), and thus the eggs are estimated to be most abundant in the environment in December and January. The value for each month for each grid-square was also summed from April to November, months when the nymphs and adults are most abundant in the environment (Doube, 1979; Barker and Walker, 2014). Grid-squares were inferred to be climatically suitable for *I. holocyclus* if the numerical value for December to March was '4' and the value for April to November was either '7' or '8'. We did this because the eggs and larvae of *I. holocyclus* are more vulnerable to desiccation than the nymphs and adults (Heath, 1974). Although the most vulnerable life stages (eggs and larvae) are most abundant in the environment

from December to March, the climate in April to November were also considered because all stages should be considered vulnerable to stressful climatic conditions, at least to some degree (Radchuk et al., 2013; Hodgson et al., 2016).

To see whether or not our climatic-range method could account for the geographic distribution of *I. holocyclus*, we 'spatially joined', with ArcGIS, the subset of 1667 records where *I. holocyclus* has been recorded (1804 records minus the 137 records from 1961 to 1990) to the projected geographic range of *I. holocyclus* from our climatic-range method.

2.5. Regions of special interest

To try and explain why *I. holocyclus* is not enzootic in Kutini-Payamu (aka Iron Range) National Park, Normanton and Dalby in Queensland, and Melbourne in Victoria, we considered in detail the climates of these regions. The climate of Toowoomba and Orbost were also studied in detail so we could think about why *I. holocyclus* is enzootic at these places, yet unable to establish in Dalby and Melbourne which are near to Toowoomba and Orbost, respectively.

2.6. Future projections for *I. holocyclus*

We projected (predicted) the geographic ranges of *I. holocyclus* in 2030, 2050, 2070 and 2090, according to the A1B and A2 climate-change scenarios from the CSIRO-Mk3 and MIROC-H climate models (Kriticos et al., 2012), with our estimated climatic-profile for *I. holocyclus* from our climatic-range method; and our CLIMEX parameters (Table 1).

3. Results

3.1. Climate accounts for the presence of *I. holocyclus*

When we executed our CLIMEX model, that is our set of climatic parameters for *I. holocyclus* (Table 1), 119 (86.9%) of our 137 records of *I. holocyclus* from 1961 to 1990 fell into grid-squares where the EI was > 0 , whereas 18 (13.1%) of our records fell into grid-squares where the EI = 0, regions that were projected to be unsuitable by our CLIMEX model (Fig. 2A). These 18 records were 0.22–103.50 km from the nearest suitable grid-square (EI > 0): mean distance $\pm$ standard deviation from the nearest suitable

grid-square was 26.38 ± 28.29 km. On the other hand, for the 1804 records of *I. holocyclus* from Barker and Barker (2018), 1685 (93.4%) of the 1804 records fell in grid-squares where the EI > 0 , whereas 119 (6.6%) of the records fell in grid-squares where the EI = 0. These 119 records were 0.17–162.98 km away from the nearest suitable grid-square: mean distance $\pm$ standard deviation from the nearest suitable grid-square was 29.36 ± 28.33 km.

Some (1595, 95.7%) of the 1667 records of *I. holocyclus* from Barker and Barker (2018) fell into grid-squares that were inferred to be climatically suitable by our climatic-range method for *I. holocyclus* whereas 72 (4.3%) of our records fell into grid-squares that were inferred to be climatically unsuitable for *I. holocyclus* (Fig. 2B). These 72 records were 0.01 km to 83.94 km away from the nearest suitable grid-square: mean distance $\pm$ standard deviation from the nearest suitable grid-square was 15.78 ± 21.94 km.

3.2. Climate accounts for the absence of *I. holocyclus* from Cape York, Normanton and Dalby in Queensland, and from Melbourne in Victoria

Our analyses of the climate at Kutini-Payamu (aka Iron Range) National Park, Cape York Peninsula, showed that the mean daily maximum temperature was too high for *I. holocyclus* from April to November; the mean daily minimum temperature was too high from March to November; and Meyer's ratio was too low in August and October for *I. holocyclus* (Fig. 3). At Normanton, the mean daily maximum temperature was too high for *I. holocyclus* for all 12 months of the year; the mean daily minimum temperature was too high in all but two of the months, June and July; and Meyer's ratio was too low from April to November for *I. holocyclus*. At Dalby, even though the mean daily minimum and maximum temperatures were within our inferred ranges for *I. holocyclus* for all 12 months of the year, the mean Meyer's ratio was too low in January, March, April and May. Similarly, for Melbourne, although the mean daily minimum and maximum temperatures were within our inferred ranges for all 12 months of the year, Meyer's ratio in January and March was too low for *I. holocyclus* (Fig. 3C). In other words, it is too dry in Melbourne in January and March, months when the larvae of *I. holocyclus* would be most abundant in the environment. On the other hand, the mean daily minimum and maximum temperatures and Meyer's ratio were within our inferred ranges for both Toowoomba and Orbost, regions where *I. holocyclus* is known to be enzootic.

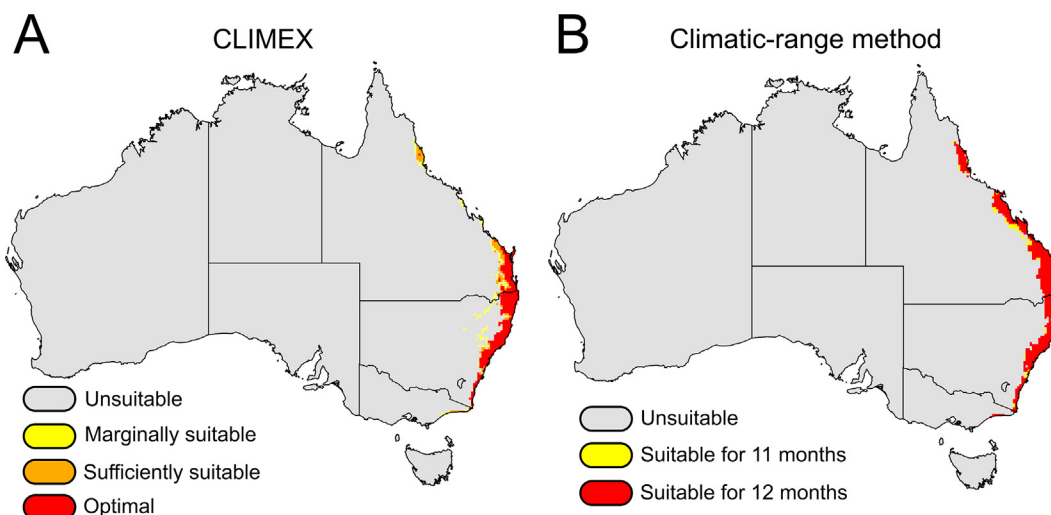


Fig. 2. The projected geographic range of *Ixodes holocyclus*, the eastern paralysis tick. (A) The projected geographic range of *I. holocyclus* by CLIMEX; and (B) the projected geographic range of *I. holocyclus* by our climatic-range method.

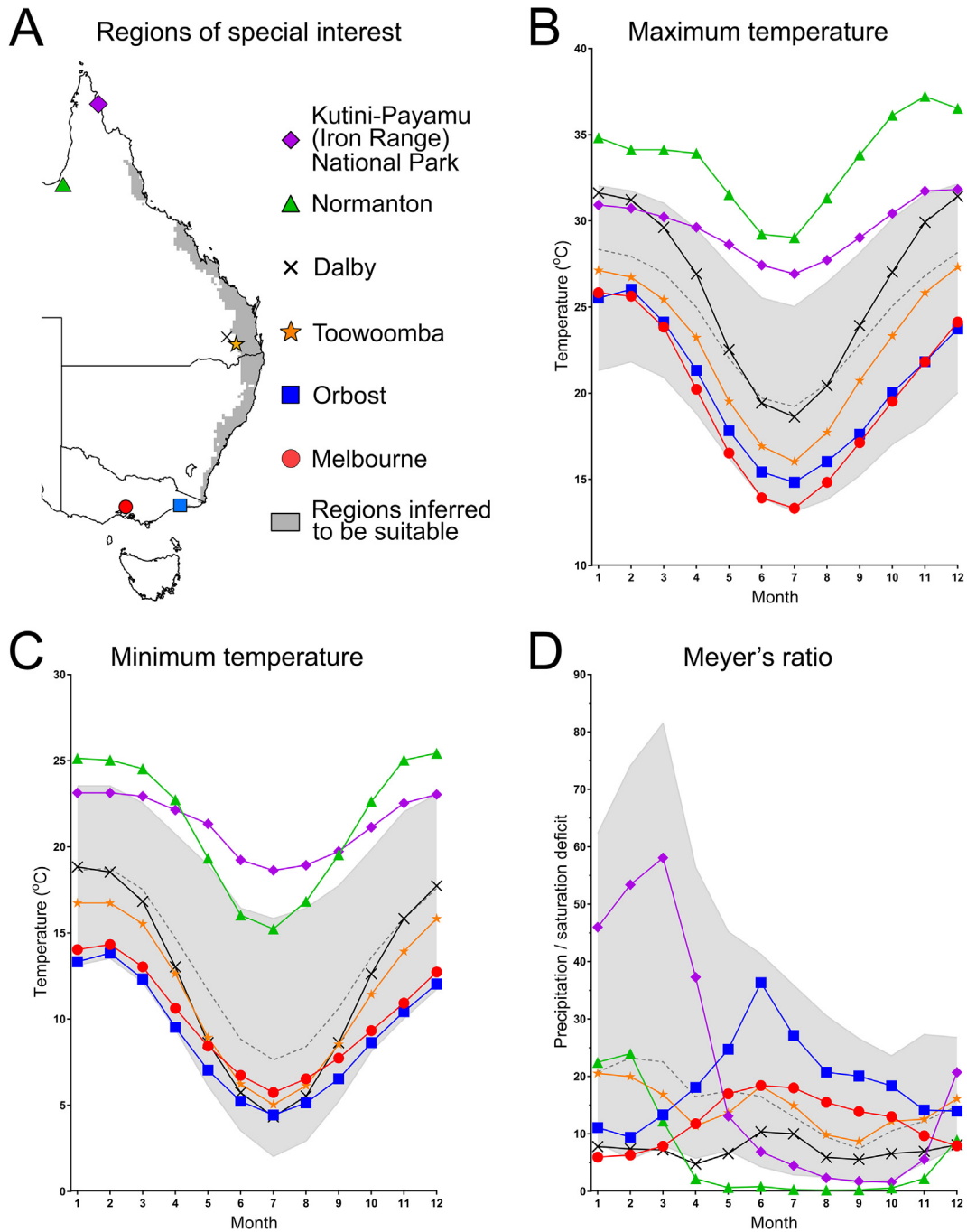


Fig. 3. The climate at the six points of special interest in the context of the climatic-range of *Ixodes holocyclus* inferred in the present study. (A) In grey, the projected geographic range of *I. holocyclus* by our climatic-range method (the present study). (B) In grey, the range of mean daily maximum temperatures that was inferred to be suitable for *I. holocyclus*; and the mean daily maximum temperatures at our six points of special interest, for all 12 months of the year. (C) In grey, the range of mean daily minimum temperatures that was inferred to be suitable for *I. holocyclus*; and the mean daily minimum temperatures at the six points of special interest, for all 12 months of the year. (D) In grey, the range of monthly Meyer's ratio that was inferred to be suitable for *I. holocyclus*; and the average monthly Meyer's ratio at the six points of special interest, for all 12 months of the year.

3.3. Future projections for *I. holocyclus* indicate that the geographic range of *I. holocyclus* may expand

Our CLIMEX model (Fig. 4) for *I. holocyclus* from the CSIRO-Mk3 climate model indicated that the geographic range (land-area; number of $10' \times 10'$ grid-squares that were climatically suitable) of *I. holocyclus* may shrink by 2090 (Table 2). On the other hand, our CLIMEX model from the MIROC-H climate model indicated that the geographic range of *I. holocyclus* may expand between 1961–

1990 and 2050 (Table 2). All four projections, however, indicated that the geographic range of *I. holocyclus* may shift south since regions in Victoria, including Melbourne, may change from unsuitable to marginal for *I. holocyclus* (Fig. 4); we note with interest that *I. holocyclus* is enzootic in some places that are presently marginal for this tick, according to our CLIMEX model e.g. Yeppoon and Mackay in Queensland (Fig. 2A).

Our climatic-range method (Fig. 5) for *I. holocyclus* from the CSIRO-Mk3 climate model indicated that the geographic range of

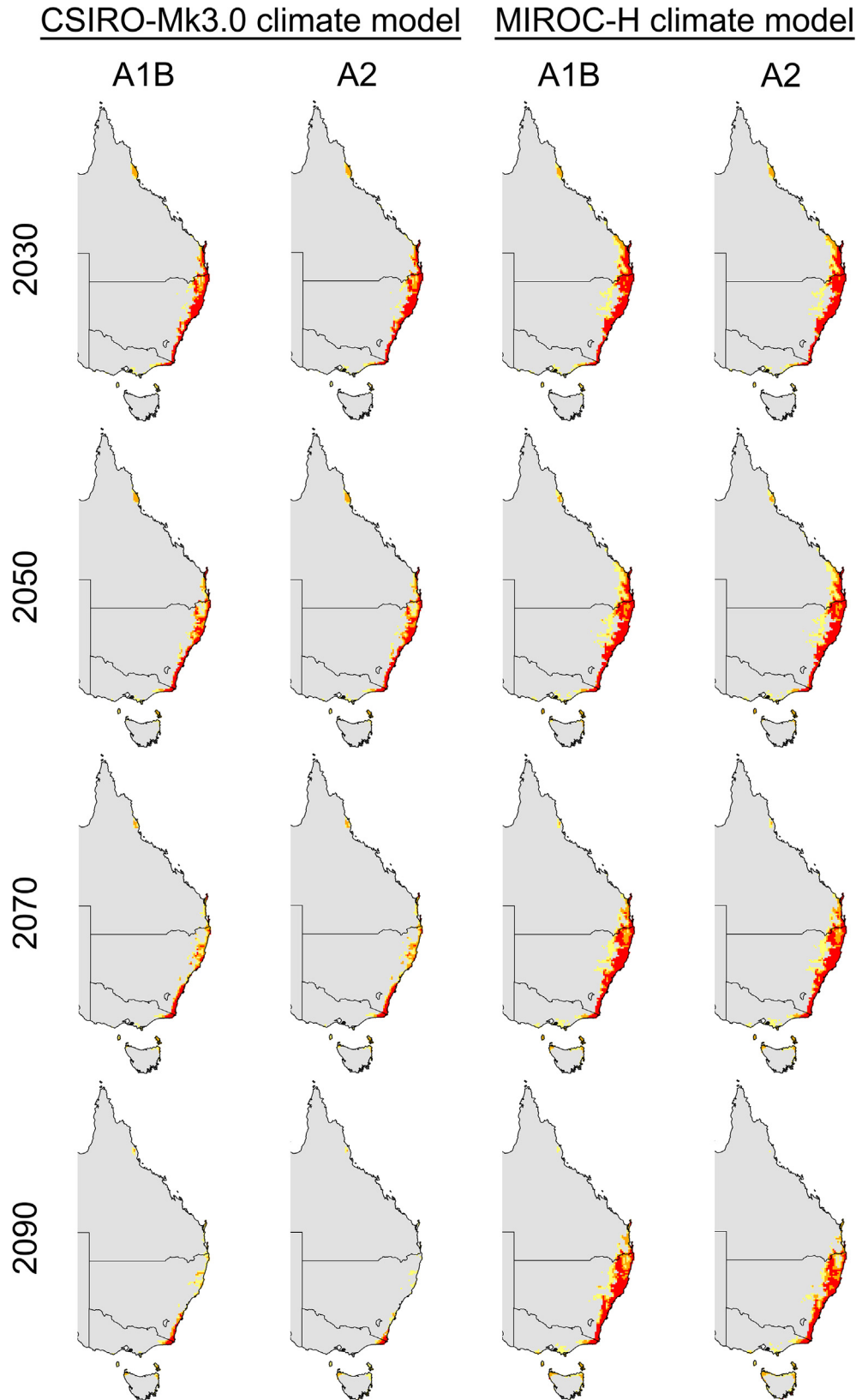


Fig. 4. Possible geographic ranges of *Ixodes holocyclus*, the eastern paralysis tick, in 2030, 2050, 2070 and 2090, inferred from our CLIMEX model for *I. holocyclus* (Table 1); darker shades indicate greater climatic suitability. The climate in these years was projected from the IPCC (Intergovernmental Panel on Climate Change, Switzerland) IV SRES (Special Report on Emissions Scenarios) A1B and A2 climate-change scenarios, from the CSIRO-Mk3 and MIROC-H climate models (Kriticos et al., 2012).

Table 2

Geographic range (land-area) projected to be suitable, climatically, for *Ixodes holocyclus*, the eastern paralysis tick of Australia, by our CLIMEX model and by our climatic-range method, for the CSIRO-Mk3 and MIROC-H climate models. Geographic range is represented by the number of $10' \times 10'$ grid-squares that were climatically suitable (CLIMEX EI > 0). Increases (+) and decreases (–) in geographic range projected to be suitable between years are in parentheses, as percentages. Geographic ranges projected to be suitable climatically in 2030 were compared with the geographic ranges projected to be climatically suitable from the average climate of 1961–1990; 2050 was compared with 2030; 2070 with 2050; and 2090 with 2070.

Geographic range of <i>Ixodes holocyclus</i> by number of grid-squares that were climatically suitable (% change between years)								
Years	CLIMEX				Climatic-range method			
	CSIRO-Mk3		MIROC-H		CSIRO-Mk3		MIROC-H	
	A1B	A2	A1B	A2	A1B	A2	A1B	A2
1961–1990	585 (NA)				709 (NA)			
2030	513 (–12.3)	523 (–10.6)	733 (+25.3)	711 (+21.5)	467 (–34.1)	497 (–29.9)	588 (–17.1)	611 (–13.8)
2050	451 (–12.1)	479 (–8.4)	767 (+4.6)	766 (+7.7)	324 (–30.6)	350 (–29.6)	501 (–14.8)	512 (–16.2)
2070	358 (–20.6)	336 (–29.9)	724 (–5.6)	730 (–4.7)	189 (–41.7)	167 (–52.3)	445 (–11.2)	442 (–13.7)
2090	246 (–31.3)	154 (–54.2)	716 (–1.1)	665 (–8.9)	54 (–71.4)	18 (–89.2)	360 (–19.1)	285 (–35.5)

NA, not applicable.

I. holocyclus may shrink by 2090 (Table 2). Similarly, our climatic-range method for *I. holocyclus* from the MIROC-H climate model indicated that the geographic range of *I. holocyclus* may shrink, albeit more gradually, compared with the CSIRO-Mk3 climate model (Table 2). All four projections, however, indicated that the geographic range of *I. holocyclus* may shrink from both the north (Queensland) and the south (Victoria), towards New South Wales (Fig. 5).

4. Discussion

Both CLIMEX and our climatic-range method were able to account for the geographic distribution of *I. holocyclus* at 93% and 96%, respectively (Fig. 2). CLIMEX indicated that the geographic range of *I. holocyclus* may shift south to include the southern coast of Victoria (Fig. 4) and may expand depending on which climate-change scenario comes to pass (Table 2). On the other hand, our climatic-range method indicated that the geographic range of *I. holocyclus* may shrink under all climate-change scenarios (Table 2).

Compared with previous studies on the geographic distribution of *I. holocyclus* (Heath, 1974; Jackson et al., 2007), our CLIMEX model and our climatic-range method were able to account for the eastern coastal distribution of *I. holocyclus* and at the same time account for the absence of *I. holocyclus* from the Cape York Peninsula and Dalby in Queensland, and regions south-west of Lakes Entrance in Victoria, including Melbourne (Fig. 2). On the other hand, regions just south of Cape York Peninsula, Toowoomba, and regions north-east of Lakes Entrance were inferred to be suitable (Fig. 2). In other words, our CLIMEX parameters and our climatic-profile of *I. holocyclus* (from our climatic-range method) allowed us to account for the presence as well as the absence of *I. holocyclus* in eastern Australia. Thus, it seems that climate explains why *I. holocyclus* has been unable to establish on Cape York Peninsula despite the presence of suitable hosts; why *I. holocyclus* is enzootic in some regions such as Toowoomba, yet absent from other regions such as Dalby, even though these regions are adjacent in Queensland; and why *I. holocyclus* is unable to establish and thus become enzootic in regions south-west of Lakes Entrance such as Melbourne, even though *I. holocyclus* has been taken here on a number of occasions by people and dogs that had visited nearby regions where *I. holocyclus* is enzootic (Beveridge, 1991; Kellers et al., 2012; Barker and Walker, 2014; Barker and Barker, 2018, 2019).

Although *I. holocyclus* is unable to establish and thus become enzootic on Cape York Peninsula and in Dalby in Queensland, and in regions south-west of Lakes Entrance such as Melbourne in Victoria, our results also indicated that these regions have climates suitable for *I. holocyclus* for some months of the year

(Fig. 3). Thus, these regions might have epizootic populations of *I. holocyclus* for some months of the year. For Kutini-Payamu (aka Iron Range) National Park on Cape York Peninsula, the climate in December, January and February was suitable for *I. holocyclus*; for Dalby, the climate in February and from June to December was suitable whereas for Melbourne, the climate in February and from April to December was suitable for *I. holocyclus* (Fig. 3). Indeed, Barker and Barker (2019, Table 1) reported 30 cases of infestation with *I. holocyclus* in the Greater Melbourne Area. Cases one to eight were apparently due to adult female ticks that had climbed onto hosts in the Greater Melbourne Area (these ticks probably moulted from nymphs to adult females in the Greater Melbourne Area) (Barker and Barker, 2019). The dates of seven of these eight cases were known: six in October, November and December; and one in June; months which our work indicated to be climatically suitable for *I. holocyclus* in Melbourne, which seems to explain how *I. holocyclus* has been recorded in the Greater Melbourne Area in certain months of the year (Barker and Barker, 2019). Moreover, it is noteworthy that our CLIMEX model for *I. holocyclus* indicated that the Greater Melbourne Area may become suitable climatically for *I. holocyclus* by 2030, depending on the climate-change scenario (Fig. 4). There is hence a possibility that *I. holocyclus* may be able to establish and thus become enzootic in the Greater Melbourne Area. On the other hand, our results from our climatic-range method indicated that the Greater Melbourne Area may remain climatically unsuitable for *I. holocyclus* (Fig. 5).

The differences among our projections for *I. holocyclus* under the climate-change scenarios are stark. On the one hand, the projections from our CLIMEX model for the MIROC-H climate model indicated that the geographic range (land-area; number of $10' \times 10'$ grid-squares that were climatically suitable) of *I. holocyclus* may expand by 2030, and again from 2030 to 2050, followed by a gradual shrink up to 2090 (Table 2). The projected geographic range of *I. holocyclus* in 2090 however, is larger than the geographic range that was projected to be climatically suitable from the average climate of 1961–1990 (Table 2). On the other hand, the projections from our CLIMEX model for the CSIRO-Mk3 climate model and our projections from our climatic-range method indicated that the geographic range of *I. holocyclus* may shrink over the coming decades (Table 2). Although our climatic-range method was able to account for a larger proportion of the geographic distribution of *I. holocyclus* at 96%, versus 93% of our CLIMEX model, we cannot conclude which method is ‘better’ or ‘more accurate’ since both CLIMEX and our climatic-range method have their respective merits. On the one hand, the CLIMEX model uses an algorithm to calculate the suitability of a location and can be inferred from the geographical distribution and calibrated from the experimental data of the species (Kriticos et al., 2017) (in the present study we

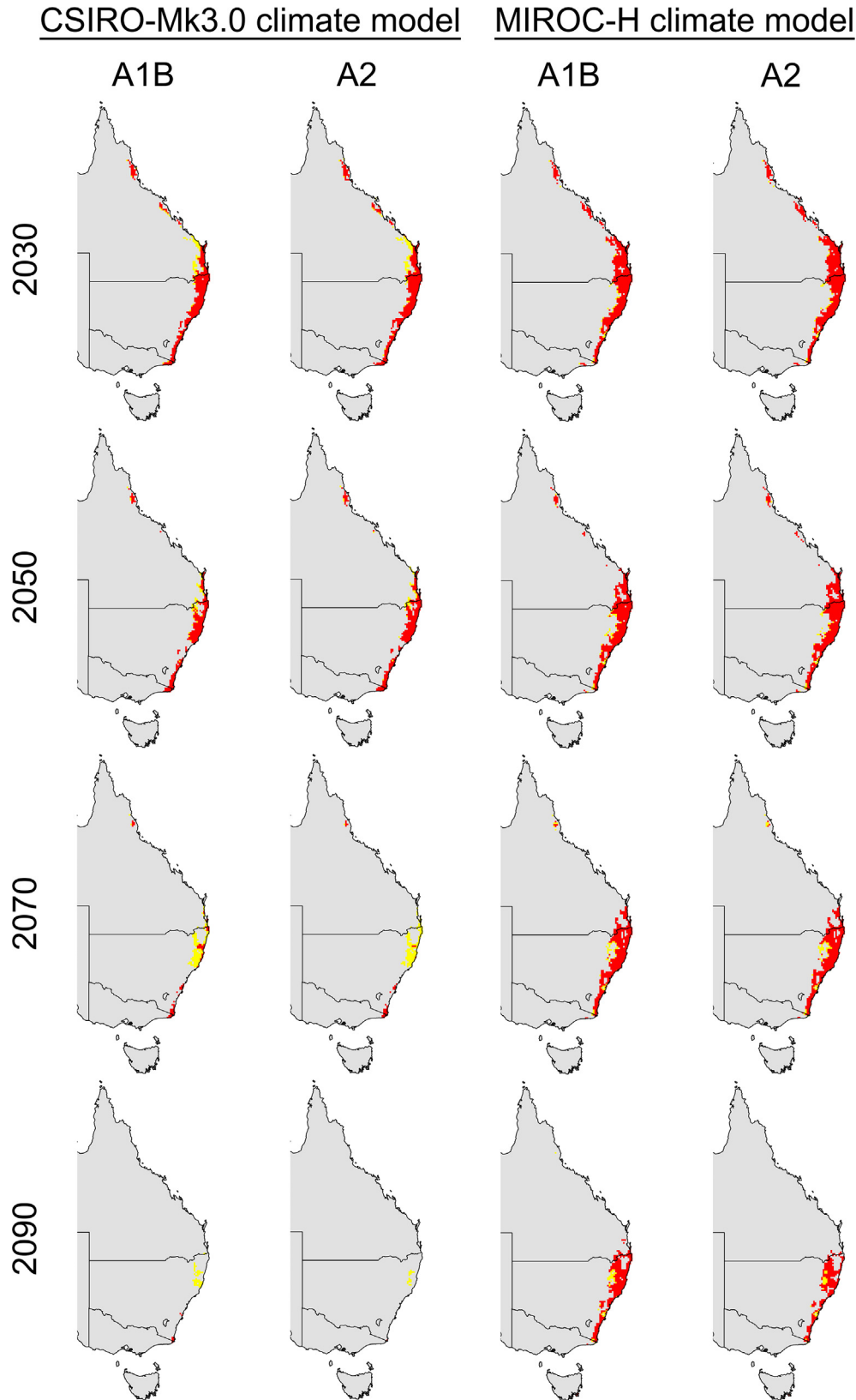


Fig. 5. Possible geographic ranges of *Ixodes holocyclus*, the eastern paralysis tick, in 2030, 2050, 2070 and 2090, inferred from our climatic-range method. Darker shades indicate greater climatic suitability. The climate in these years was projected from the IPCC (Intergovernmental Panel on Climate Change, Switzerland) IV SRES (Special Report on Emissions Scenarios) A1B and A2 climate-change scenarios, from the CSIRO-Mk3 and MIROC-H climate models (Kriticos et al., 2012).

used experimental data from Heath (1974) and inferred the other parameters from the geographical distribution). On the other hand, our climatic-range method is a simple, inferential, rule-based approach which does not use any algorithms and is thus more parsimonious.

Similar to any other species distribution models, our CLIMEX model and our climatic-range method for *I. holocyclus* did not consider the availability of food/hosts, which for *I. holocyclus*, are mainly marsupial hosts. Although *I. holocyclus* is considered to be catholic in its feeding habits, having been recorded to feed, apparently to repletion in at least some cases, on at least 30 different species of animals, including humans (Roberts, 1970; Barker and Walker, 2014), the abundance (density) of these hosts in regions that are climatically suitable for *I. holocyclus* is not well known.

We thus conclude that climate accounts for the presence, as well as the absence, of *I. holocyclus*, the eastern paralysis tick, throughout regions in eastern Australia. Moreover, with increasing temperatures and decreasing moisture availability, the geographic range of *I. holocyclus* may shrink over the next few decades, or the geographic range may continue to expand to 2050, depending on which climate-change scenario comes to pass.

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