Global Change Biology (2002) **8,** 954–971

Potential changes in the distributions of latitudinally restricted Australian butterfly species in response to climate change

LINDA J. BEAUMONT and LESLEY HUGHES
Department of Biological Sciences, Macquarie University, North Ryde, 2109, NSW, Australia

Abstract

This study assessed potential changes in the distributions of Australian butterfly species in response to global warming. The bioclimatic program, BIOCLIM, was used to determine the current climatic ranges of 77 butterfly species restricted to Australia. We found that the majority of these species had fairly wide climatic ranges in comparison to other taxa, with only 8% of butterfly species having a mean annual temperature range spanning less than 3 °C.

The potential changes in the distributions of 24 butterfly species under four climate change scenarios for 2050 were also modelled using BIOCLIM. Results suggested that even species with currently wide climatic ranges may still be vulnerable to climate change; under a very conservative climate change scenario (with a temperature increase of 0.8–1.4 °C by 2050) 88% of species distributions decreased, and 54% of species distributions decreased by at least 20%. Under an extreme scenario (temperature increase of 2.1–3.9 °C by 2050) 92% of species distributions decreased, and 83% of species distributions decreased by at least 50%. Furthermore, the proportion of the current range that was contained within the predicted range decreased from an average of 63% under a very conservative scenario to less than 22% under the most extreme scenario.

By assessing the climatic ranges that species are currently exposed to, the extent of potential changes in distributions in response to climate change and details of their life histories, we identified species whose characteristics may make them particularly vulnerable to climate change in the future.

Keywords: BIOCLIM, bioclimatic envelope, butterflies, climate change, lepidoptera, range shifts

Received 9 July 2001; revised version received 22 October 2001 and accepted 7 November 2001

Introduction

Since the 1970s, global mean annual temperature has increased approximately 0.15 °C per decade (Hulme & Sheard, 1999). Pre-instrumental proxy climate data suggest that the last 100 years, and in particular the last decade, were the warmest of the last millennium (Mann *et al*., 1999). By the end of this century global mean annual temperature is projected to rise 1.4–5.8 °C (IPCC, 2001).

This prediction has lead to widespread concern about the possible effects of climate change on species' distributions, abundance, and interactions. The life histories and fitness of ectotherms such as insects, that rely on external heat sources and sinks to regulate their body temperature, are strongly influenced by temperature and precipitation. Temperature influences the rates of biochemical reactions, and basic metabolic functions of ectotherms may change dramatically in response to fairly small changes in temperature (Dawson, 1992). Hence, temperature influences the consumption and developmental rate of insects (Scriber & Lederhouse, 1983; Gilbert, 1984; Casey, 1993; Ayres & Scriber, 1994; Drake, 1994; Stamp & Bowers, 1994; Liu *et al*., 1995; Buse *et al*., 1999), fitness, distribution, and migration (Drake, 1994; Liu *et al*., 1995), voltinism (Pollard & Yates, 1993), larval emergence (Dewar & Watt, 1992; Buse & Good, 1996; Sparks & Yates, 1997; Buse *et al*., 1999), and survival (Taylor, 1988). Furthermore, high ambient temperature reduces the time required for insects to raise their body temperature to the flight activity threshold (Drake, 1994). As a result, flight-dependent activities such as

Correspondence: Linda Beaumont, tel. (612) 9850 8191, fax (612) 9850 8245, e-mail: lbeaumon@rna.bio.mq.edu.au

mate-location, hill-topping (Wickman, 1988), and egg laying, may increase (Jones *et al.*, 1982; Dennis, 1993). Elevated temperature may also lower survival if the species' temperature threshold is exceeded (Dennis, 1993).

As for other insects, temperature and moisture strongly regulate the life cycle of lepidoptera. The distribution and abundance of butterflies appears to be influenced by climate, and in particular, temperature (Pollard, 1988; Dennis, 1993; Pollard & Yates, 1993; Sparks & Yates, 1997). For example, in Britain and Finland, there is a close association between species richness and climatic variables, suggesting that a change in climate may result in species ranges shifting (Dennis, 1993; Virtanen & Neuvonen, 1999). As climate changes, species are hypothesised to be affected in several ways: (a) distributions may shift polewards as low latitude areas become less climatically favourable, and high latitude areas become more favourable (Parmesan, 1996; Parmesan *et al.*, 1999; Hughes, 2000); (b) populations and species at low latitudes may be more prone to extinction than those at high latitudes (Kristiansen, 1993), and (c) insects may undergo earlier larval emergence and prolonged flight periods (Kristiansen, 1993).

Preliminary data suggest that such responses have already occurred among some butterfly species found in the Northern Hemisphere. Conspicuous range expansions have occurred in some British lepidoptera since the 1970s (Pollard *et al.*, 1995, 1996), and while poleward range expansions have been recorded for numerous other European lepidoptera (Hill *et al.*, 1999; Parmesan *et al.*, 1999), only a small proportion of species appear to have shifted to lower latitudes (Parmesan *et al.*, 1999). A census of populations of Edith's checkerspot butterfly, *Euphydras editha*, indicated a significant altitudinal and latitudinal cline in population extinctions along the west coast of North America, with populations in Mexico being four times more likely to have become extinct than those in Canada (Parmesan, 1996). Further, since 1975, the flight peak of microlepidoptera in the Netherlands has occurred, on average, almost 12 days earlier (Ellis *et al.*, 1997; Kuchlein & Ellis, 1997). Shifts toward earlier flight dates have also been recorded in British Lepidoptera (Pollard, 1991), where it has been estimated that a warming of 1 °C may advance flight dates by 2 to 10 days (Roy & Sparks, 2000).

Although studies such as these have detected a range of responses in some species of butterflies to changes in climate experienced so far, field and laboratory experiments alone will never be sufficient to determine the potential responses of large numbers of species. Therefore, there is a growing need to use bioclimatic models to assess potential changes in species distributions, and to identify those species that may be most vulnerable to climate change. Bioclimatic models enable species to be studied either individually, or en-masse, and for hypotheses to be developed regarding factors that may limit distributions. These models attempt to match the current distribution of a species with a number of climatic variables, producing an envelope that describes the climate within a species' current range. The parameters of the climatic envelope can then be used to estimate potential changes in distribution under various climate change scenarios (e.g. see Bennett *et al.*, 1991; Hughes *et al.*, 1996; Eeley *et al.*, 1999).

In this study, we used bioclimatic modelling to determine the potential responses of a large group of endemic Australian butterfly species to climate change. Butterflies were chosen for several reasons. First, the strong effect of temperature on butterflies and recent evidence of shifts in the distribution and flight phenology of butterfly species from the Northern Hemisphere indicate that these taxa may be vulnerable to climate change. Second, Australia has already experienced significant warming; air temperatures have risen 0.5–0.9 °C since the beginning of the 20th century (Salinger *et al.*, 1996), which is slightly higher than the global average of 0.6 °C (IPCC, 2001). Precipitation patterns have also changed (Nicholls & Lavery, 1992) along with the frequency and intensity of El Niño events (Salinger *et al.*, 2000). Over the next 50 years, mean annual temperatures in Australia are predicted to rise between 0.8 and 3.9 °C, depending upon CO_2 emission rates, while precipitation is expected to decrease over much of the continent (Hulme & Sheard, 1999). Third, butterflies are one of the few insect taxa in Australia for which good distribution records exist, due to their conspicuousness and popularity with collectors. Over 110 000 location records of approximately 400 species of butterflies found in Australia have been compiled in the Dunn & Dunn, National Database of Australian Butterflies (for details see Dunn & Dunn, 1991). Records were collated from both public and private collections, as well as the published literature. For many species, records date back to the early 20th century. This database, along with the bioclimatic model, BIOCLIM v 5.0 (Houlder *et al.*, 1999), was used to investigate three issues:

(*i*) *Climatic envelopes of species*. We modelled the climatic envelopes of 77 latitudinally restricted species, making this the largest bioclimatic study of Australian invertebrates. The climatic envelope of a species enables us to identify those species who may be at risk from future warming by comparing their current climatic range to the magnitude of predicted climatic changes. Previous studies have shown that a large number of Australian eucalypts (Hughes *et al.*, 1996) and endangered vertebrates (Bennett *et al.*, 1991) may soon be faced with temperature and precipitation patterns to which they are not currently exposed.

(*ii*) *Potential changes in species' distributions*. As the climate changes, Australian butterfly species may respond by shifting their distributions, as have some European and North American species. We modelled the potential changes in the distributions of 24 of the original 77 species in response to four climate change scenarios for 2050.

(*iii*) *Identification of vulnerable species*. We examined characteristics of species' life histories, the width of their climatic envelope, and potential changes in their distributions to identify those that may be most vulnerable to climate change.

Methods

Bioclimatic model

Bioclimatic models are descriptive and/or predictive tools that can be used to describe the climate within a species' current distribution, to identify other locations that have the same climate as that found in a species' current distribution, and to estimate how distributions may change in relation to future climate.

BIOCLIM (Houlder *et al*., 1999) uses climate surfaces generated from long-term monthly averages of climate variables at over 900 temperature stations and 11 000 precipitation stations throughout Australia (Busby, 1991). Provided the latitude, longitude and elevation of a location is known, its climate can be interpolated (for a full description of BIOCLIM, see Nix, 1986; Houlder *et al*., 1999). Predictive error is usually less than 10% of the monthly precipitation values and 5% for mean maximum and minimum temperature values (Nix, 1986). Using five climatic variables (maximum temperature, minimum temperature, rainfall, radiation, evaporation) for all known locations of the species in question, BIOCLIM derives monthly values for 35 parameters that describe the bioclimatic range occupied by a species, and produces a climatic envelope for that species (see Nix, 1986). Each bioclimatic parameter can be expressed in percentiles, hence areas within a species range where populations are not exposed to climatic extremes ('core areas') can be determined. For the purpose of this study, core areas were defined as locations where values of all bioclimatic parameters were within the 2.5–97.5% values (95th percentile range). These locations were considered to possess a climate suitable for the species. If values for one or more parameters fell outside this range, but were within the total climatic range, the climate was considered to be marginal, and locations were termed 'range areas'. Conversely, if values for any parameter lay outside the total range, then the area was deemed climatically unsuitable for the species in question.

In order to use BIOCLIM as a predictive system, a Digitial Elevation Model (DEM) was required. BIOCLIM summarised the climate within each grid cell of the DEM, then identified all cells in the climatic grid that fitted within the parameters of the species' climatic envelope. This produced the *current potential climatic distribution* of a species, i.e. all locations where the species in question may occur if climate alone determines distribution.

To assess how a species may shift its distribution under a particular climate scenario, a new climatic grid was generated, which incorporated seasonal temperature and precipitation changes from the climate change scenarios. Again all cells within the new climatic grid that contained a suitable climate for each species were identified, hence indicating how a species range may shift in response to climate change.

Climate change scenarios

The Climatic Research Unit (CRU) at the University of East Anglia supplied climate change scenarios for the year 2050. These scenarios were chosen for three reasons. First, they were the most up-to-date scenarios available. Second, the scenarios were at a higher spatial resolution than previous scenarios for Australia, with a gridbox of 2.5° latitude by 3.75° longitude. Third, the scenarios provided changes in mean summer, autumn, winter, and spring temperature and precipitation.

The four scenarios used will be referred to as very conservative, conservative, low extreme, and high extreme scenarios, respectively (Table 1). The scenarios relate to four levels of future greenhouse gas emissions defined by the IPCC, with atmospheric CO_2 levels by 2050 ranging from 480 p.p.m.v. in the very conservative scenario to 560 p.p.m.v. in the high extreme scenario (Hulme & Sheard, 1999). The scenarios represent the median response of 10 global climate model simulations, performed by seven climate laboratories located in six countries (Hulme & Sheard, 1999). Changing sulphate aerosol concentrations were not considered, and scenarios assumed that there were no climate policy implementations. The 10 models sometimes yielded different regional climate responses, and naturally, there is uncertainty in these models. In addition, Tasmania and many coastal areas were treated as ocean, not land, by most of the models used to create these scenarios, and this may affect the climate change signal (J. Crossley CRU, pers comm.). Values for temperature were expressed as the change in °C from the average 1961–1990 climate, while precipitation was the per cent change from the average 1961–1990 climate (Hulme & Sheard, 1999).

The scenarios indicate that by 2050 average annual temperatures across Australia may be up to 3.9 °C

Table 1 Estimated increases in atmospheric CO_2 concentrations, global mean annual temperature (MAT), and mean annual temperature and precipitation (MAP) within Australia for 2050 (Hulme & Sheard, 1999). Different regions in Australia are predicted to change at varying rates, hence MAT increase and MAP decrease are shown as ranges

Scenario	CO_2 increase (p.p.m.v.)	Global MAT increase (°C)	Australian MAT increase (°C)	Australian MAP decrease (%)
Very conservative	479	0.9	0.8–1.4	0–18
Conservative	492	1.5	1.2–2.2	0–29
Low extreme	555	1.8	1.4–2.6	0–34
High extreme	559	2.6	2.1–3.9	0–59

warmer than at present. Temperature increases are predicted to be greatest in summer and spring, and increase more rapidly in continental Australia than coastal areas. Most of Australia may be affected by a decrease in rainfall in summer, while in winter, seasonal rainfall in parts of south-western and central Australia may decline by more than 50%. Conversely, rainfall in north-east Queensland may not change significantly compared to the natural 30-year variability.

(*i*) *Derivation of butterfly species climatic envelopes.* Approximately 400 species of butterflies are found in Australia, of which around 173 are restricted to this continent. A major aim of our study is to identify species that may be vulnerable to climate change. Hence, as it is well recognised that species with narrow distributions may be vulnerable (Peters & Darling, 1985), criteria for inclusion in this study were that species be restricted to Australia, and have a distribution spanning less than 20° latitude. Further, in order to produce climatic envelopes, each species had to have records of their known distribution in the Dunn and Dunn National Database of Australian Butterflies. Ultimately, 77 species from five families were chosen: Hesperiidae (21 species), Lycaenidae (27 species), Nymphalidae (21 species), Papilionidae (1 species), Pieridae (7 species) (nomenclature in accordance with Common & Waterhouse 1981). The latitude and longitude of known locations for species were derived from Dunns' Database.

Distributions of all species were mapped in a Geographic Information System (Unix Arc/Info v7.2) (ArcInfo V. 7.2 (1999)) and compared to maps in *Butterflies of Australia* (Common & Waterhouse, 1981) to identify anomalous points that may have resulted from incorrect geocoding or identification. Questionable locations were removed from further analysis.

The elevation of all locations was derived using a DEM developed by the Australian National University, Aus40. DEM (AUS40.DEM (1999)), which has a resolution of 1/40 of a degree (approximately 2.5 km^2). This DEM has an accuracy of $+/-10$ m in relatively flat topography and $+/-100$ m in mountainous regions (D. Houlder, pers comm.). Temperature ranges and rainfall ratios (highest rainfall : lowest rainfall) were calculated. Relationships between the latitudinal extent of species' known ranges and both their temperature range and precipitation ratios were analysed using the statistical package, SPSS (v8.0.2) (SPSS v 8.0.2 (1998)).

(*ii*) *Potential changes in the distributions of species.* We modelled the potential changes in the distributions of 24 of the original 77 species in response to four climate change scenarios. These species were chosen because they have very restricted distributions (spanning less than 15° latitude), and together are found in a wide range of habitat types.

The potential distribution of each species under each climate change scenario was classified into range and core areas, and mapped in ArcView (v3.0) (ArcView V3.0 (1999)). Changes in the latitudinal width of each species' range and core areas under each climate change scenario were calculated and expressed as a per cent increase or decrease in latitudinal extent. The number of BIOCLIM grid cells in a species distribution can be used as an approximation of area, hence we compared the change in the number of grid cells in the potential distribution of a species under each climate change scenario to that species' current potential climatic range. Results were expressed as a per cent increase or decrease in the size of range and core areas. Furthermore, to determine the extent to which species may have to shift their distributions in response to climate change, we calculated the proportion of grid cells present in each climate change scenario that were also present in each species current potential climatic range. Results are given for each species entire distribution, and for those locations classified as core areas. The relationship between changes in distribution size, latitudinal width, and mean annual temperature range and precipitation ratios were analysed using multiple regression in SPSS.

(*iii*) *Identification of Vulnerable Species.* Peters & Darling (1985) identified characteristics of species that may make them vulnerable to a changing climate. These included

(1) species that are narrowly distributed or geographically localised, (2) habitat specialists, (3) alpine species, (4) poor dispersers, (5) genetically impoverished species, and (6) species with peripheral and/or disjunct populations. Species with these characteristics may be vulnerable to climate change because the probability of finding new habitats with suitable climates, and surviving in these areas, may be low. Of the 77 species studied, we identified species with at least two of the above characteristics and which also had either: (i) very narrow climatic ranges or (ii) were predicted to lose large proportions of their current climatic range under the climate change scenarios. We classified these species as potentially vulnerable to climate change.

Results

(i) Species climatic envelopes

The majority of the 77 endemic Australian butterfly species we studied encounter a wide range of temperature and precipitation conditions within their range (Table 2). Only six species (8%) have a mean annual temperature range of less than 3 °C (Fig. 1). As temperature may be elevated beyond this by 2050, these species may be left without a suitable bioclimate within their current range. CRU scenarios for 2080 suggest that under high CO_2 conditions, temperatures in Australia may rise in excess of 6 °C. This could potentially result in 18 species (23%) experiencing mean annual temperatures beyond those to which they are currently exposed. Only two species (3%) have less than a 1.2-fold range of mean annual precipitation. As such, few species as a whole would be directly affected by decreases in rainfall of 20%, although many local populations may be at risk (Fig. 2).

As expected, regressions indicated that there was a statistically significant relationship between the latitudinal extent of species known distributions and the mean annual temperature range they experience ($r^2 = 0.277$, $P < 0.001$, $n = 77$). However, latitudinal range did not have a significant relationship with precipitation ratios ($r^2 = 0.035$, $P = 0.102$, $n = 77$).

(ii) Potential changes in species' distributions in response to climate change

Our bioclimatic models indicated that the distributions of the majority of the 24 butterfly species modelled may decrease in size and latitudinal extent as the intensity of climate change increases (Figs 3a–d and 4a–d), due to range contractions at both the northern and southern boundaries (Table 3). Furthermore, our models suggested that future ranges may become more fragmented compared to the current potential climatic range (for example, the predicted distributions of *Tisiphone helena* in Fig. 5).

Changes in latitudinal width The very conservative climate change scenario for 2050 suggests that the latitudinal extent of two of the 24 species studied (*Trapezites macqueeni* and *Tisiphone helena*) may expand as climate changes, although the latitudinal extent of both species distributions may contract under the more extreme scenarios (Table 4). Three species may have a negligible response (*Jalmenus daemeli, Prosotas felderi, Hypocysta euphemia*). However, the remaining 19 species may suffer a decrease in the latitudinal extent of their range. Significantly, four of these species (*Anisynta sphenosema, Chaetocneme porphyropis, Hypochrysops halyaetus, Jalmenus inous*) may have the latitudinal extent of their range contract by more than 20% of their current climatic range (Fig. 3a–d). Should climate match that of the most extreme climate change scenario, then 21 of the 24 species may suffer a decrease in their latitudinal extent, and nine may decrease in excess of 20% (*A. sphenosema*, *A. tillyardi*, *C. porphyropis*, *Exometoeca nycteris*, *Trapezites heteromacula*, *H. halyaetus*, *J. eichhorni*, *J. inous*, *Appias melania*).

Core areas are locations within the 2.5th to 97.5th percentiles of the species climatic envelope, that is, areas where climatic extremes are not met. Populations may be more likely to persist in these locations. However, the latitudinal extent of core areas decreased dramatically with increasing severity of climate change. Under each of the four scenarios, 2, 6, 7 and 15 species lost more than 20% of the latitudinal extent of core areas, respectively (Fig. 3a–d).

Changes in area As with latitudinal extent, the general pattern that emerged from this study was that the majority of species may undergo a decrease in range size (Fig. 4a–d). However, changes in area (number of BIOCLIM grid cells) indicated a much stronger effect of global warming on butterfly species' distributions than that estimated by latitudinal width (Fig. 3a–d). For example, *Nesolycaena albosericea* loses only a small proportion of its latitudinal extent under the very conservative scenario (1.6%) and gains slightly under the high extreme scenario (0.5%). However, under these two scenarios, *N. albosericea* may lose 20–66% of the actual size of its range, due to a decrease in longitudinal distribution and range fragmentation (Table 4). Similarly, the latitudinal extent of *T. macqueeni* is estimated to increase slightly under the very conservative scenario, and yet the size of this species distribution under the same scenario decreases by 43%.

In the very conservative scenario, range sizes of three butterfly species are estimated to increase (*A. sphenosema, E. nycteris, T. helena*), while core areas increased for two of

Table 2 Climatic envelopes of 77 endemic Australian butterfly species. The latitudinal range of each species was derived from the Dunn & Dunn National Database of Australian Butterflies (Southern Hemisphere: north = low latitude, south = high latitude). The mean annual, maximum, and minimum temperature and precipitation, plus the temperature range and precipitation ratio (highest:lowest) were derived using BIOCLIM

	Latitude				Temperature				Precipitation		
Species	North	South	Range	MAT	Max	Min	Range	MAP	Max	Min	Ratio
Hesperiidae											
Anisynta cynone	29.3	37.2	7.9	15.7	17.8	9.6	8.2	507	1505	331	4.5
A. dominula	29.9	42.6	12.8	9.2	16.6	3.3	13.3	1285	2869	520	5.5
A. monticolae	33.8	38.0	4.2	10	13.9	3.3	10.6	1148	2530	630	4
A. sphenosema	28.7	35.0	6.3	17.1	19.5	14.7	4.8	828	1141	437	2.6
A. tillyardi	26.7	32.1	5.5	13.5	17.4	9.7	7.7	1123	1862	735	2.5
Chaetocneme beata	16.8	34.5	17.7	18.3	24.5	13.7	10.8	1358	2183	694	3.1
C. denitza	10.7	28.1	17.4	21.9	27.5	17.4	10.1	1293	2183	666	3.3
C. porphyropis	16.1	19.0	2.9	21.8	24.5	19	5.5	2330	4187	1216	3.4
Dispar compacta	24.4	39.0	14.7	13.5	19.6	6.7	12.9	1008	1953	574	3.4
Euschemon rafflesia	15.5	32.4	17.0	19.4	24.5	14.4	10.1	1642	3376	665	5.1
Exometocea nycteris	31.5	35.0	3.5	16.6	17.9	15.1	2.8	904	1112	341	3.3
Trapezites argenteoornatus	20.4	33.3	12.9	19.6	25.2	16.7	8.5	594	930	199	4.7
T. heteromacula	10.2	19.2	9.1	24	26.3	19.9	6.4	1670	2183	939	2.3
T. iacchoides	28.7	37.5	8.9	14	17.2	9.7	7.5	1171	1862	760	2.5
T. iacchus	10.6	30.0	19.4	22.3	26.3	18.2	8.1	1402	2088	643	3.2
T. luteus	23.7	43.4	19.7	14	21.8	8.6	13.2	745	1619	337	4.8
T. macqueeni	13.4	19.8	6.4	21.9	25.4	19	6.4	1387	2037	803	2.5
T. petalia	16.8	34.6	17.8	18.9	23.9	14.5	9.4	1064	2037	520	3.9
T. phigalioides	28.5	38.5	10.1	12.3	18.3	6.4	11.9	1027	2094	574	3.6
T. praxedes	26.0	39.1	13.1	16.1	20.2	10.8	9.4	1233	1834	799	2.3
T. sciron	31.3	36.6	5.3	15.6	18	12.9	5.1	572	1118	240	4.7
Lycaenidae											
Candalides cyprotus	21.9	36.5	14.6	16.8	24.1	9.2	14.9	849	1412	244	5.8
C. gilberti	11.2	17.9	6.8	26.6	27.6	25.6	2	1295	1570	672	2.3
Hypochrysops epicurus	23.6	32.9	9.3	19.6	22	16.8	5.2	1496	1864	901	2.1
H. halyaetus	24.4	32.1	7.7	18.6	22.1	17	5.1	658	1053	214	4.9
H. hippuris	12.7	12.8	0.1	25	25	24.7	0.3	1767	1778	1732	1
H. miskini	15.3	28.2	12.9	21.4	24.5	19	5.5	1679	3523	1050	3.4
H. piceata	28.0	28.0	0.1	17	17.2	16.5	0.7	660	662	649	1
Jalmenus clementi	20.7	22.8	2.1	24.2	26.1	23	3.1	310	351	277	1.3
J. daemeli	16.9	30.5	13.6	19.6	24.5	12.8	11.7	836	2183	470	4.6
J. eichhorni	10.7	18.1	7.4	24.7	26.2	19.9	6.3	1605	1851	747	2.5
J. evagoras	21.1	38.2	17.1	15.4	22.3	5.6	16.7	969	1984	586	3.4
J. icilius	21.5	38.5	17.0	15.7	25.8	10.9	14.9	586	1094	195	5.6
J. inous	24.9	34.0	9.1	17.2	21.9	15.6	6.3	823	1053	216	4.9
J. lithochroa	31.7	35.1	3.4	15.9	18.3	15	3.3	487	646	223	2.9
J. pseudictinus	16.8	27.9	11.1	19.7	23.7	17.5	6.2	1003	2126	630	3.4
Neolucia hobartensis	30.0	43.5	13.5	7.9	13.7	3.3	10.4	1593	2530	521	4.9
N. mathewi	31.5	41.5	10.0	14.3	17.2	3.3	13.9	1246	2530	703	3.6
Nesolycaena alboscericea	23.7	27.5	3.8	7.9	13.7	3.3	10.4	1593	2530	521	4.9
N. urumelia	11.9	18.6	6.7	26.7	27.6	25.1	2.5	1183	1559	497	3.1
Ogyris aenone	10.6	28.0	17.5	20.2	26.3	16.5	9.8	1209	2245	633	3.5
O. barnardi	20.2	33.0	12.9	18.7	23.2	10.9	12.3	546	1576	209	7.5
O. ianthis	25.0	34.0	9.0	16.9	18.2	14.4	3.8	936	1298	593	2.2
O. idmo	29.3	38.4	9.1	15.9	19.7	12.3	7.4	775	1178	329	3.6
O. iphis	12.5	20.7	8.3	22	27.3	19.4	7.9	1428	1953	589	3.3
O. otanes	29.3	36.4	7.1	15.8	19.7	12.9	6.8	524	881	237	3.7
Prosotas felderi	24.5	34.5	10.1	18.4	21.2	10.4	10.8	1263	2070	633	3.3
Pseudalmenus chlorinda	30.4	43.1	12.7	11.7	16.4	5.6	10.8	1004	2252	513	4.4

Table 2 (continued)

Nymphalidae											
Argynnina cryila	28.1	39.1	11.0	12.9	18.3	3.3	15	1135	2530	350	7.2
A. hobartia	41.0	43.6	2.6	9.3	12.3	5	7.3	1313	2949	517	5.7
Geitoneura acantha	23.8	38.7	14.9	14	20.1	5.6	14.5	989	1882	528	3.6
G. minyas	26.2	35.0	8.8	17.7	21.3	12.9	8.4	698	1148	206	5.6
Heteronympha banksii	26.7	39.1	12.4	13.5	18	8.7	9.3	1124	2070	592	3.5
H. cordance	30.0	43.6	13.6	9.7	15.4	3.3	12.1	1351	2922	554	5.3
H. mirifica	26.5	37.6	11.1	16.4	19.8	9.7	10.1	1274	2419	666	3.6
H. paradelpha	28.6	38.5	10.0	12.8	17	7.9	9.1	1111	1984	643	3.1
H. penelope	28.2	43.6	15.4	11.1	16.4	3.3	13.1	1069	2715	520	5.2
H. solandri	33.7	39.1	5.4	9.3	13.4	3.3	10.1	1404	2530	748	3.4
Hypocysta euphemia	28.2	37.3	9.1	15.3	18.3	10.3	8	1132	2070	693	3
H. irius	10.7	29.7	19.0	22.4	26.2	16.8	9.4	1661	3582	693	5.2
H. pseudirius	16.8	35.3	18.5	17.7	23.2	11.3	11.9	1047	1915	576	3.3
Nesoxenica leprea	41.0	43.5	2.6	7.9	11.8	4.3	7.5	1770	2960	685	4.3
Oreixenica correae	35.4	37.9	2.5	7.6	12.8	3.3	9.5	1683	2530	809	3.1
O. kershawi	31.8	38.7	6.9	11.2	16.4	3.3	13.1	1221	2530	656	3.9
O. lathoniella	28.8	43.6	14.7	10	14.4	3.3	11.1	1275	2922	540	5.4
O. latialis	33.9	37.5	3.6	7.2	12.5	3.3	9.2	1602	2530	501	5
O. orichora	35.4	42.2	6.9	6.6	12.5	3.3	9.2	1682	2530	641	3.9
O. ptunarra	41.4	42.5	1.1	7.9	11	5.4	5.6	894	2478	452	5.5
Tisiphone helena	16.1	21.2	5.1	21.9	24.5	17.5	7	2017	3602	470	7.7
Papillionidae											
Ornithoptera richmondia	25.5	31.9	6.4	18.5	20.8	14.4	6.4	1679	2327	1053	2.2
Pieridae											
Appias melania	14.0	23.1	9.2	22.4	24.8	18.2	6.6	1859	3376	965	3.5
Delias harpalyce	28.2	38.8	10.6	13.4	19	6.7	12.3	948	1906	349	5.5
Elodina angulipennis	19.0	33.9	14.9	18.2	23.7	9.7	14	1304	2070	632	3.3
E. perdita	12.8	21.2	8.4	22.8	25	19.2	5.8	1473	1981	953	2.1
E. queenslandica	9.6	25.4	15.8	23.8	26.7	18.8	7.9	1645	2363	747	3.2
E. tongura	11.0	14.0	3.0	26.1	27	25.4	1.6	1184	1449	1067	1.4
E. walkeri	10.2	17.5	7.4	26.1	27.5	21.7	5.8	1467	3425	756	4.5

these species (*A. sphenosema*, *E. nycteris*). However, under both of the conservative scenarios, 13 species and 19 species may lose at least 20% of their distribution, respectively. Significantly, in the conservative scenario, with a mean annual temperature increase of between 1.2 and 2.2 °C, *C. phorphyropis* loses all of its core areas. In the high extreme scenario, all but two species (*E. nycteris*, *J. inous*) are estimated to suffer a decrease in range size, with 20 species estimated to lose more than 50% of their current potential climatic range, while 21 species may lose more than 50% of their current core areas.

Changes in similarity As scenarios become progressively more extreme, the number of cells that remain suitable under both the current climate and the predicted climate decreases (Fig. 6a–d). On an average, 63% of cells currently suitable remain so under the very conservative scenario. Under the high extreme scenario, on average 80% of cells that are climatically suitable lie outside areas that are currently suitable. This becomes more severe with core areas, with on average, only 14% of currently suitable core areas remaining so by 2050 under the high extreme scenario.

As expected, there is a positive relationship between the size and latitudinal width of species current potential climatic ranges, and mean annual temperature ranges (size: $r^2 = 0.512$, $P < 0.001$, $n = 24$; latitudinal extent: $r^2 = 0.343$, $P = 0.003$, $n = 24$). As climate change scenarios become more extreme, the relationship between per cent change in the latitudinal width of species distributions and mean annual temperature range becomes stronger, such that species with narrower temperature ranges lose a greater proportion of the latitudinal width of their distribution (very conservative scenario: $r^2 = 0.153$, $P = 0.059$, $n = 24$; conservative scenario: $r^2 = 0.25$, $P = 0.013$, $n = 24$; low extreme scenario $r^2 = 0.358$, $P = 0.002$, $n = 24$; high extreme scenario: $r^2 = 0.373$, $P = 0.002$, $n = 24$).

(iii) Identification of vulnerable species

Of the original 77 species studied, seven were identified as most vulnerable to climate change: the hesperiids

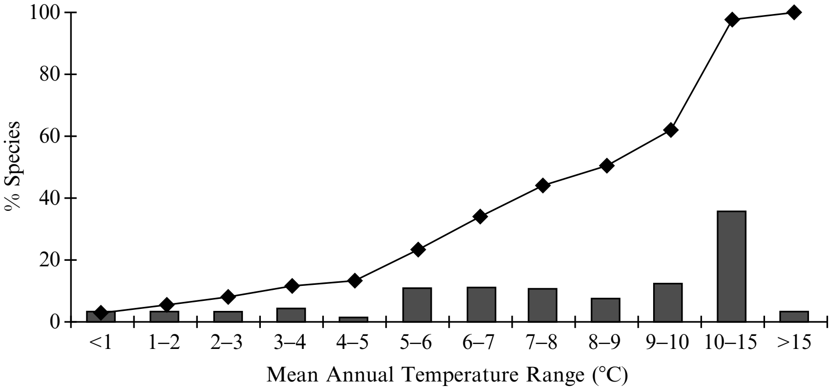

Fig. 1 Frequency distribution (dark bars) and cumulative frequency distribution (line) of the mean annual temperature ranges of 77 latitudinally restricted Australian butterfly species.

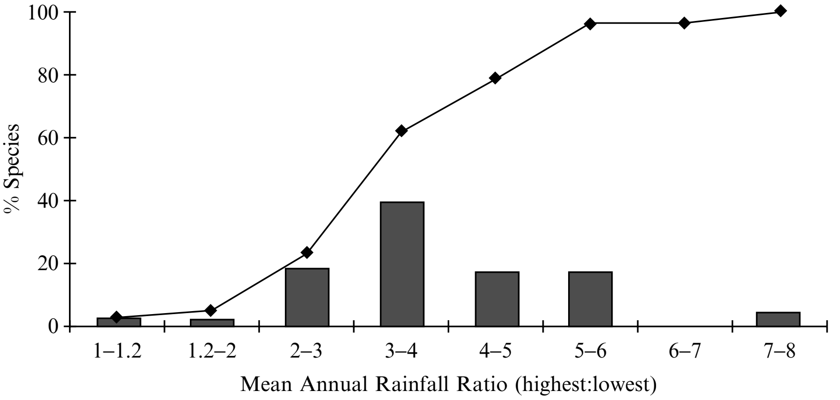

Fig. 2 Frequency distribution (dark bars) and cumulative frequency distribution (line) of the mean annual precipitation ranges (highest average rainfall:lowest) for 77 latitudinally restricted Australian butterfly species.

Exometocea nycteris and *Trapezites heteromacula*, and the lycaenids *Hypochrysops halyaetus, H. piceata, Jalmenus clementi, J lithchroa,* and *Nesolyceana urumelia* (Table 5). Each of these species have a number of characteristics that suggested they may have difficulty adjusting to climate change. First, five species (*E. nycteris, H. piceata, J. clementi, J. lithochroa,* and *N. urumelia*) have very narrow climatic envelopes, with mean annual temperature ranges spanning less than 4 °C. Climate change scenarios indicated that mean seasonal temperature by 2050 may exceed values to which these species are currently exposed. Second, of the 24 species for which range shifts under the climate change scenarios were modelled, two species (*T. heteromacula* and *H. halyaetus*) lost large proportions of the size of their distributions under all scenarios (Table 4). Third, these species include habitat specialists, mutualists, and poor dispersers, and all currently have narrow geographical distributions.

Discussion

Bioclimatic modelling indicates that climate change may have adverse effects on the geographical ranges of a large number of endemic Australian butterfly species from a diverse range of habitat types, even though many species currently have large climatic ranges.

(i) Climatic envelopes of species

The climatic envelopes and geographic ranges of butterfly species were large in relation to previous studies on Australian flora and fauna such as eucalypts (Hughes *et al.*, 1996), and vertebrates (Bennett *et al.*, 1991). As expected, there was a significant positive relationship between the size and latitudinal extent of butterfly species known distributions, and the mean annual temperature range within these areas.

(ii) Potential changes in distributions

Statistical analyses supported the hypothesis that as climate change becomes more extreme, species with narrower geographic distributions, and hence narrower climatic ranges, will suffer greater latitudinal range contractions than those with wider geographic and climatic ranges. However, our models demonstrated that even species with wide climatic ranges may still lose substantial

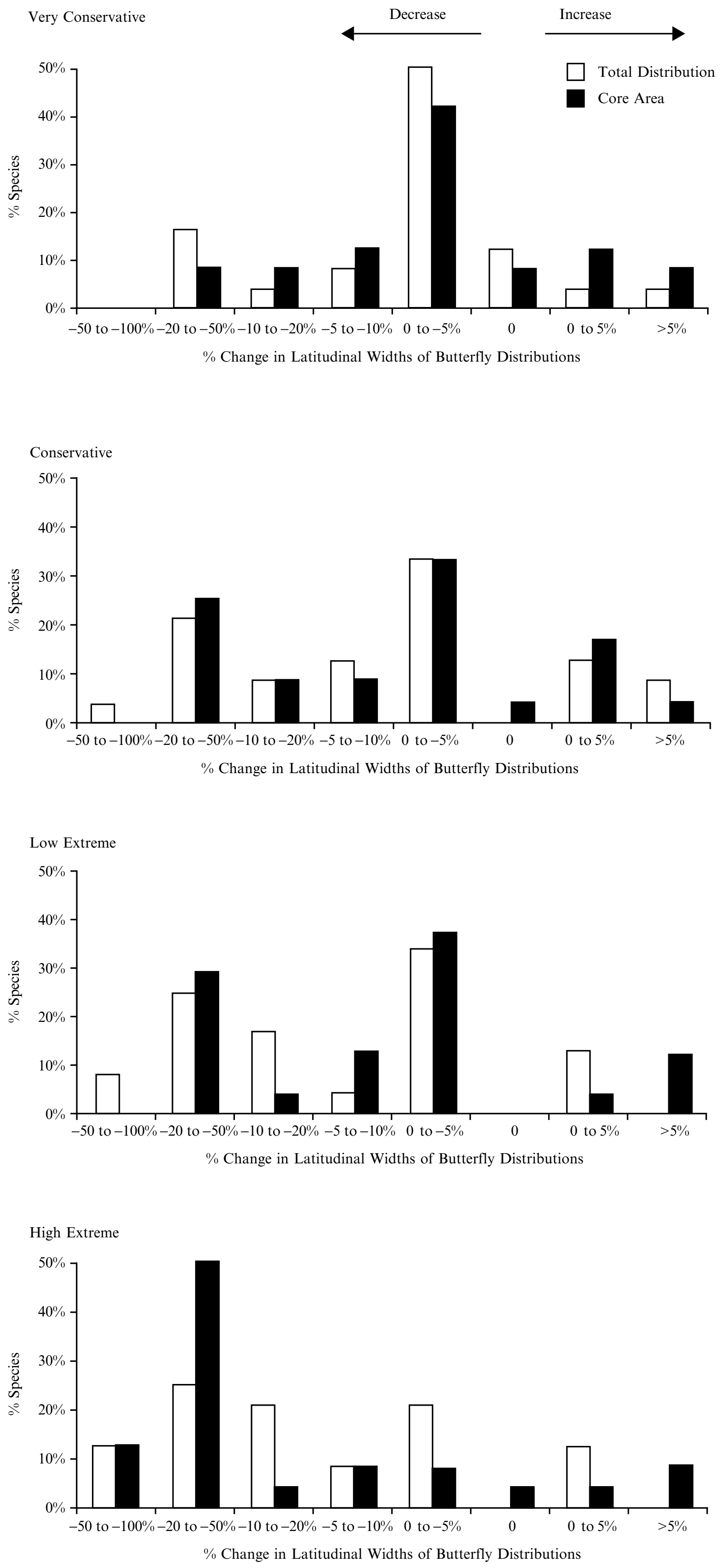

Fig. 3 (a)–(d) Change in the latitudinal width of 24 butterfly species distributions, in response to four climate change scenarios. Results are expressed as the percentage change in latitudinal width of distributions under the climate change scenario, compared to each species current potential climatic range as determined by BIOCLIM. Results are given for both total distribution (light bars) and core areas (dark bars), which are those locations where climatic parameters lie within the 2.5th to 97.5th percentiles of the species' climatic envelopes.

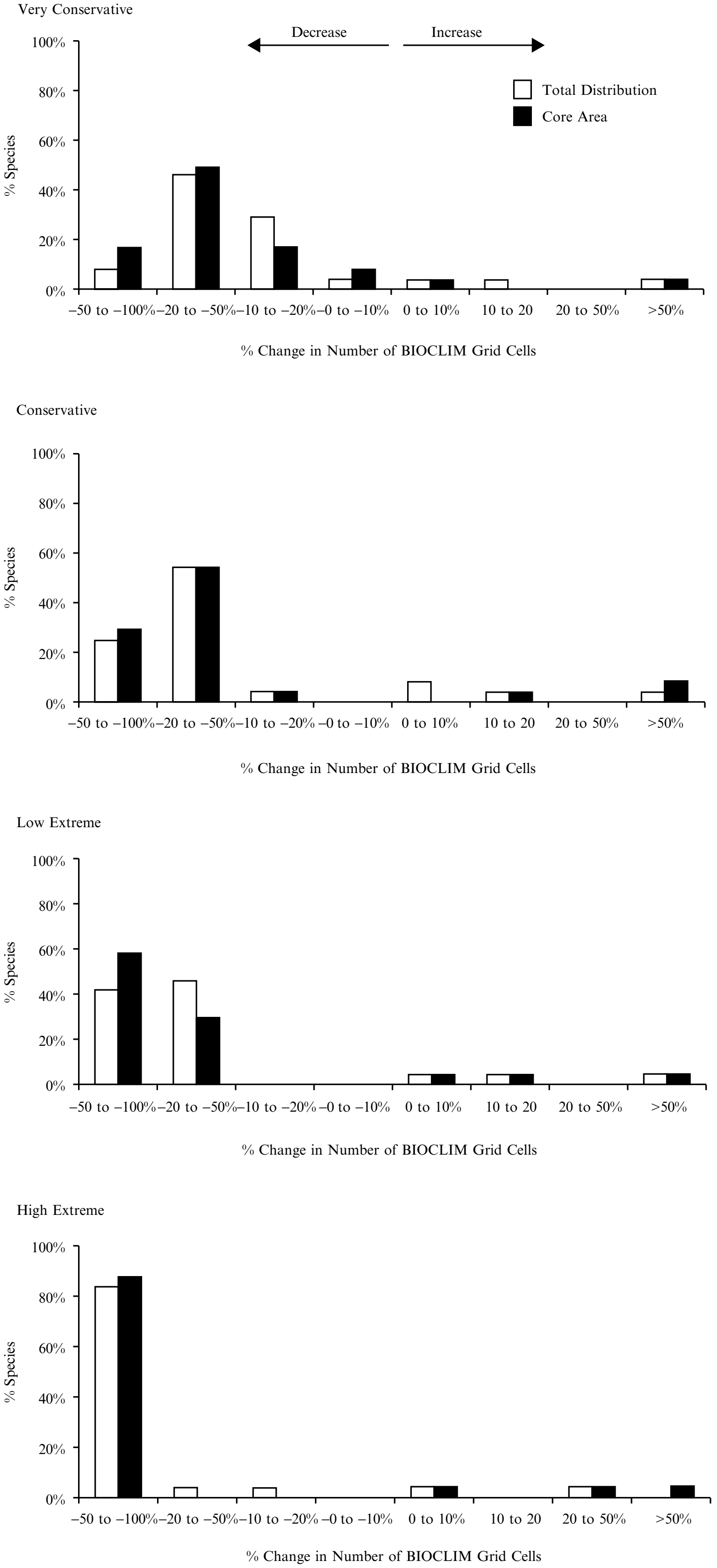

Fig. 4 (a)–(d) Change in the number of BIOCLIM grid cells of 24 butterfly species distributions, in response to four climate change scenarios. The number of grid cells approximates area, and the results are expressed as the percentage change in number of cells under each climate change scenario, compared to the number of cells in each species current potential climatic range. Results are shown for the percentage change in the total size of distributions (light bars), and change in core areas (dark bars), which are locations where climatic parameters lie within the 2.5th to 97.5th percentiles of the species climatic envelopes.

Table 3 Mean change in latitude at which 24 butterfly species' northern and southern edges are predicted to occur, in response to four climate change scenarios for 2050 (standard deviation in brackets). Positive values for species northern boundaries suggest that this edge may move to higher latitudes (polewards) in response to a changing climate, while negative values for species southern boundaries suggest that this edge may move to lower latitudes in response to climate change, with the net result being a range contraction

Climate change scenario	Change in degree latitude of northern range limit	Change in degree latitude of southern range limit
Very conservative	0.41 (0.96)	−0.13 (0.32)
Conservative	0.61 (1.35)	−0.16 (0.67)
Low extreme	0.87 (1.58)	−0.35 (0.83)
High extreme	1.31 (2.03)	−0.37 (0.78)

proportions of their potential distribution. For example, *Neolucia mathewi* has a mean annual temperature range and precipitation ratio of 13.9 °C and 3.6, respectively, and yet this species was estimated to lose almost 27% of its current potential climatic range under the very conservative scenario, and as much as 77% under the high extreme scenario.

The bioclimatic models indicated that two of the 24 species modelled (*Anisynta sphenosema* and *Exometoeca nycteris*) may benefit from global warming. These species are currently restricted to south-western Western Australia, a region predicted to increase in temperature from between 0.9 and 3.4 °C and decrease in precipitation by up to 28% by 2050 (Hulme & Sheard, 1999). The models suggest that under global warming, similar climatic conditions may be found in South Australia, resulting in more climatically suitable habitat for these two species. However, it is doubtful that these species are capable of migrating in excess of 1000 km across a very arid environment to take advantage of climatically suitable habitat in South Australia.

Maps of the potential changes in the distributions of the 24 butterfly species indicated that not only do distributions decrease in area, but climatically suitable patches may also become increasingly isolated. Furthermore, as the magnitude of future change becomes greater, the proportion of species' predicted distributions that coincide with their current potential climatic range decreases dramatically, indicating that species may need to shift their distributions to take advantage of other climatically suitable areas.

Our results also suggest that the southern (high latitude) margins of species ranges will, on average, move to slightly lower latitudes, while the northern (low latitude) margins will shift polewards, thus resulting in range contractions. This is in contrast to observations of some Northern Hemisphere species, where the northern boundary has shifted polewards with little change in the southern boundary, thus resulting in range expansions for some species (Parmesan *et al*., 1999).

(iii) Identification of vulnerable species

We identified seven endemic Australian butterfly species that may be at particular risk from a changing climate; *E. nycteris, T. meteromacula, H. halyaetus, H. piceata, J. clementi, J. lithochroa,* and *N. urumelia*. The narrow geographic and climatic ranges of most of these species plus their inability to migrate and general life history characteristics (Common & Waterhouse, 1981; Kitching *et al*., 1999) suggests they may be unlikely to shift their distributions to track either a changing climate or concurrent changes in the distribution of their host plants.

With the exception of *N. urumelia*, the lycaenids (*H. halyaetus*, *H. piceata, J. clementi,* and *J. lithochroa*) are obligate myrmecophiles; hence for a shift in distribution to be possible, these butterflies must find habitats that are not only climatically suitable but which also have requisite larval food plants and mutualistic ant species. Populations of *N. urumelia*, *J. clementi, J. lithochroa* and *T. heteromacula* are very localised, often reflecting the patchy occurrence of their preferred habitat. *Hypochrysops piceata* and *J. lithochroa,* in particular, are threatened by habitat destruction (Braby, 2000). *Exometoeca nycteris* is from a monotypic genera, and its lack of close relatives suggests that this species is relictual (Braby, 2000).

Under each of the four climate change scenarios, *H. halyaetus* and *T. heteromacula* consistently suffered greater range contractions than the other 22 species for which distributions were modelled. *Hypochrysops halyaetus* is restricted to coastal and subcoastal areas of Western Australia where colonies are found in heathland and are fairly localised. Our models suggest that this species may lose between 58% and 99% of its current climatic range, depending upon the magnitude of change. Less that 27% of its predicted distribution under the very conservative scenario occurs in locations that the species may currently occupy.

Only a slight increase in temperature is required to reduce the distribution of the rare *Trapezites heteromacula*

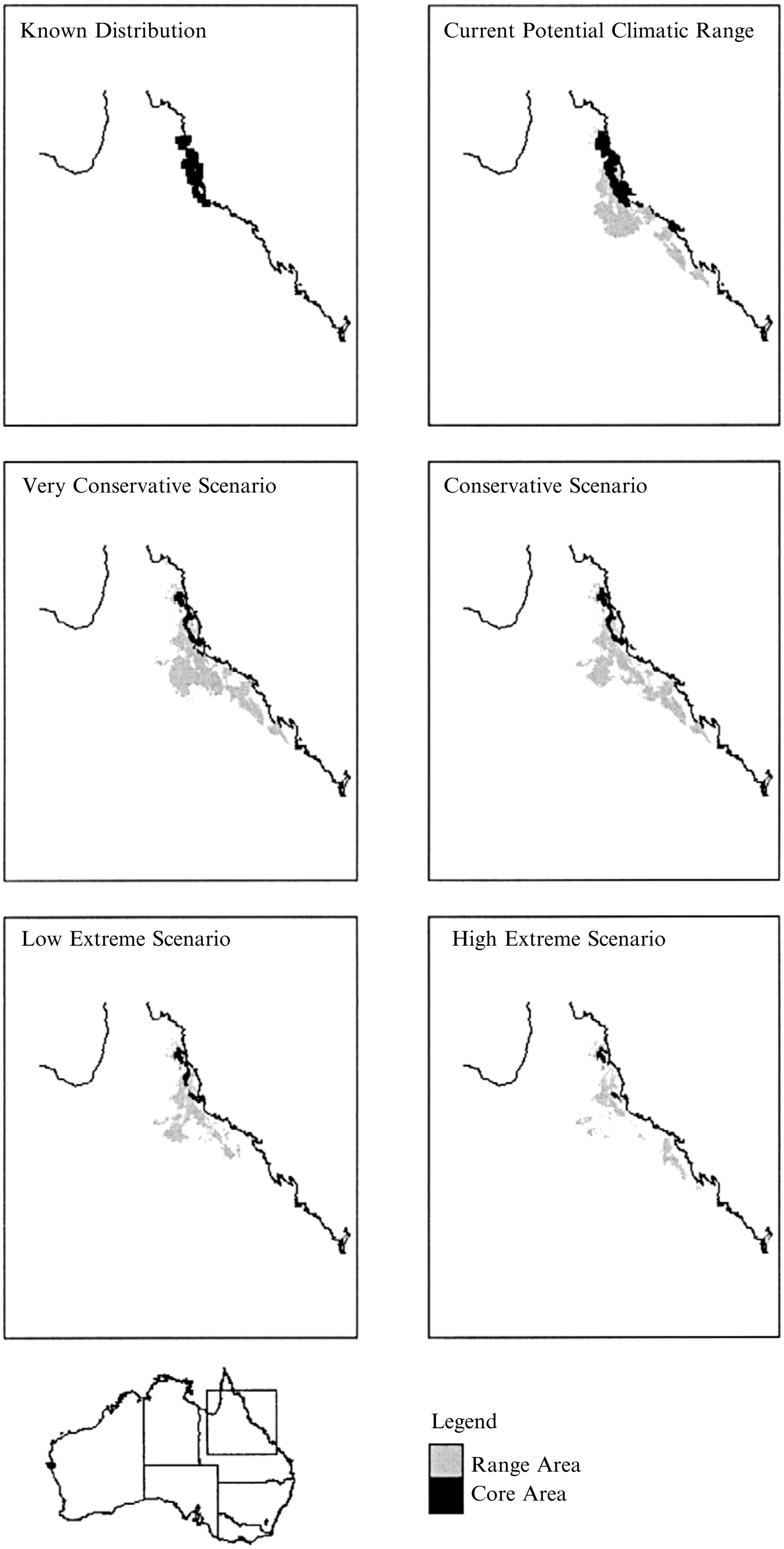

Fig. 5 These maps identify the current known distribution of *Tisiphone helena,* as well as the current potential distribution, i.e. all areas identified by BIOCLIM that contain a bioclimate suitable for *T. helena.* The potential changes to this species distribution under four climate change scenarios for 2050 are also mapped. Locations containing suitable bioclimate are identified as either range or core areas (which are those locations where climatic parameters lie within the 2.5th to 97.5th percentiles of the species climatic envelope).

Table 4 Approximate increase or decrease in the latitudinal extent and area (number of BIOCLIM grid cells) of 24 butterfly species distributions in response to four climate change scenarios for 2050. Results are expressed as the percentage change compared to each species current potential distribution, and are given for both range and core areas. The percentage similarity for each species total distribution and core areas are also given, i.e. the proportion of grid cells within a predicted distribution that are also climatically suitable in the species current potential climatic range

	% Change in Latitudinal Width								% Change in Number of BIOCLIM Cells								% Similarity							
	Very Conservative		Conservative		Low Extreme		High Extreme		Very Conservative		Conservative		Low Extreme		High Extreme		Very Conservative		Conservative		Low Extreme		High Extreme	
Species	Range	Core	Range	Core	Range	Core	Range	Core	Range	Core	Range	Core	Range	Core	Range	Core	Total	Core	Total	Core	Total	Core	Total	Core
Hesperiidae																								
Anisynta monticolae (Mountain skipper)	−3.0	−3.4	−8.5	−6.2	−11.6	−9.6	−14.8	−46.6	−23.8	−18.1	−42.7	−35.7	−54.9	−49.2	−76.0	−72.4	74.1	77.3	55.2	60.0	43.5	46.6	22.3	22.9
A.sphenosema (Wedge skipper)	−25.1	−4.0	−32.0	−11.6	−52.1	−39.2	−54.8	−66.8	2.6	2.9	3.3	13.4	2.5	15.6	−12.0	1.9	64.2	61.7	52.4	48.5	50.2	45.8	38.1	33.1
A.tillyardi (Tillyard's skipper)	−3.1	−3.1	−7.8	−7.8	−5.9	−5.9	−41.2	−92.2	−22.7	−15.4	−38.3	−34.6	−44.5	−42.7	−73.2	−77.6	76.4	77.5	59.1	56.2	52.7	48.3	25.6	19.6
Chaetocneme porphyropis (Purple Brown-eye)	−28.5	−28.5	−32.8	−32.8	−36.6	−36.6	−48.4	−48.4	−40.9	−39.1	−48.5	−100.0	−61.1	−60.0	−78.5	−76.4	49.3	49.7	38.3	36.9	26.2	25.2	8.5	8.4
Dispar compacta (Dispar skipper)	−3.2	1.7	−3.9	3.6	−3.9	−3.8	−5.1	−5.7	−16.1	−21.9	−30.7	−39.2	−39.2	−49.4	−60.2	−69.2	81.8	71.7	65.5	52.0	56.9	42.6	36.5	23.7
Exometoeca nycteris (Western flat)	−9.9	−8.6	−24.5	−19.4	−25.2	−18.7	−27.2	−20.9	100.0	108.2	102.1	129.5	92.0	121.0	43.8	68.2	39.3	39.7	17.1	16.2	13.2	12.0	3.0	1.9
Trapezites heteromacula (Orange white-spot skipper)	−19.3	−15.5	−34.7	−31.6	−38.9	−36.1	−44.0	−41.3	−62.9	−54.6	−71.6	−64.6	−77.9	−72.4	−90.3	−87.5	34.3	40.0	25.5	30.0	19.2	22.2	6.8	7.1
T.iacchoides (Iacchoides skipper)	−0.8	0.0	−0.8	0.0	−4.1	−0.3	−4.1	−0.3	−30.0	−31.4	−48.9	−52.7	−61.9	−68.2	−79.2	−82.1	66.5	65.9	47.0	44.5	35.1	30.1	18.5	14.4
T.macqueeni (Macqueen's skipper)	0.9	−0.4	8.8	−0.4	−12.4	−0.4	−15.9	−4.4	−43.0	−29.3	−55.3	−38.6	−61.8	−45.3	−73.9	−60.1	56.1	68.6	44.1	59.4	37.5	52.3	25.5	37.9
Lyceanidae																								
Hypochrysops epicurus (Dull Jewel)	−1.0	5.2	−9.1	4.7	−4.7	4.3	−19.1	0.8	−28.3	−3.8	−40.6	−41.7	−47.6	−48.5	−74.7	−75.9	63.9	70.2	51.0	28.3	43.1	21.2	17.2	0.5
H. halyaetus (Western jewel)	−23.2	−46.2	−28.1	−34.0	−31.6	−34.0	−94.2	−100.0	−58.6	−88.4	−84.3	−96.9	−90.9	−98.6	−98.8	−100.0	26.4	9.6	5.0	1.5	0.7	0.3	0.0	0.0
Jalmenus daemeli (Damel's blue)	0.0	−2.2	1.3	−1.1	1.3	−0.8	1.8	−25.3	−8.6	−30.0	−22.1	−47.9	−33.6	−58.4	−60.5	−75.9	90.8	69.2	76.8	50.7	64.7	40.0	35.6	20.0
J. eichhorni (Northern imperial blue)	−8.1	−7.9	−11.3	−21.9	−22.4	−23.2	−25.1	−29.5	−44.8	−56.1	−60.2	−65.5	−66.5	−74.9	−79.8	−89.5	52.2	35.8	36.4	22.6	30.2	14.8	17.1	2.8

Table 4 (continued)

	% Change in Latitudinal Width								% Change in Number of BIOCLIM Cells								% Similarity							
	Very Conservative		Conservative		Low Extreme		High Extreme		Very Conservative		Conservative		Low Extreme		High Extreme		Very Conservative		Conservative		Low Extreme		High Extreme	
Species	Range	Core	Range	Core	Range	Core	Range	Core	Range	Core	Range	Core	Range	Core	Range	Core	Total	Core	Total	Core	Total	Core	Total	Core
J. inous (Inous blue)	−39.7	−13.0	−55.9	−30.8	−67.5	−34.2	−72.5	−39.7	−10.6	−59.0	5.6	−10.4	12.6	7.8	7.1	22.9	41.9	24.2	26.1	9.9	26.3	7.6	16.8	0.3
Neolucia mathewi (Mathew's blue)	−4.2	−0.3	3.5	−0.3	3.5	−7.1	2.3	−22.8	−26.8	−39.6	−52.6	−69.4	−60.5	−76.8	−76.9	−91.7	70.7	56.6	44.6	29.6	36.4	21.6	18.8	6.9
Nesolycaena alboserícea (Satin blue)	−1.6	2.9	−1.0	2.9	3.1	−1.7	0.5	11.6	−20.6	−20.0	−36.6	−35.2	−49.4	−66.4	−66.0	−70.8	70.3	66.6	53.4	42.6	41.8	23.8	22.7	6.4
Prosotas felderi (Felder's lineblue)	0.0	−2.3	−1.2	−2.3	−3.9	−3.4	−3.6	−30.7	−16.3	−3.6	−38.0	−28.2	−48.7	−41.1	−70.9	−60.9	80.7	85.5	58.8	59.8	48.2	48.2	27.9	29.1
Nymphalidae																								
Argynnina cryila (Cryil's brown)	−3.0	−2.5	−0.8	−1.8	−3.6	50.4	−4.0	−6.5	−18.4	−36.1	−27.6	−48.5	−30.3	−56.0	−43.7	−74.6	18.4	0.0	11.8	0.0	26.3	13.5	6.3	0.0
Heteronympha mirifica (Wonder brown)	−2.2	−0.2	−3.9	−2.3	−4.6	−4.4	−3.7	−13.5	−19.5	−12.5	−35.2	−35.5	−45.8	−49.7	−65.4	−70.4	79.0	78.1	14.5	50.8	52.7	37.3	32.4	13.9
Hypocysta euphemia (Rock ringlet)	0.0	0.0	5.0	3.8	−0.3	5.2	−2.1	13.7	−17.7	−29.7	13.9	83.4	−43.3	−61.2	−64.9	−84.2	81.4	61.2	63.3	39.9	54.5	28.6	32.2	10.0
Oreixenica correae (Correa brown)	−1.9	27.0	−2.8	29.7	−10.4	17.6	−18.9	0.0	−17.5	−10.2	−38.1	−39.7	−52.1	−53.9	−70.9	−71.0	80.9	88.6	61.0	59.5	47.4	45.6	28.9	27.7
Tisiphone helena (Helena brown)	15.0	−6.3	17.0	−38.1	−14.0	−43.4	−7.6	−43.9	11.4	−35.1	−12.1	−46.0	−46.5	−56.2	−66.2	−68.5	88.6	60.5	67.7	49.6	39.3	39.8	29.1	27.5
Papilionidae																								
Ornithoptera richmondia (Richmond birdwing)	−4.2	1.0	−4.6	−4.4	−5.0	−4.4	−11.1	−35.1	−20.0	−42.9	−42.2	−61.0	−49.7	−81.0	−71.9	−90.4	76.7	52.4	52.5	34.0	42.3	14.9	19.2	5.0
Pieridae																								
Appias melania (Gray Albatross)	−1.6	−0.5	−15.6	−0.5	−30.6	−2.3	−30.6	−46.8	−43.4	−33.3	−53.0	−47.5	−61.9	−58.6	−77.5	−74.9	55.3	60.3	45.7	46.1	35.8	35.4	21.2	19.5

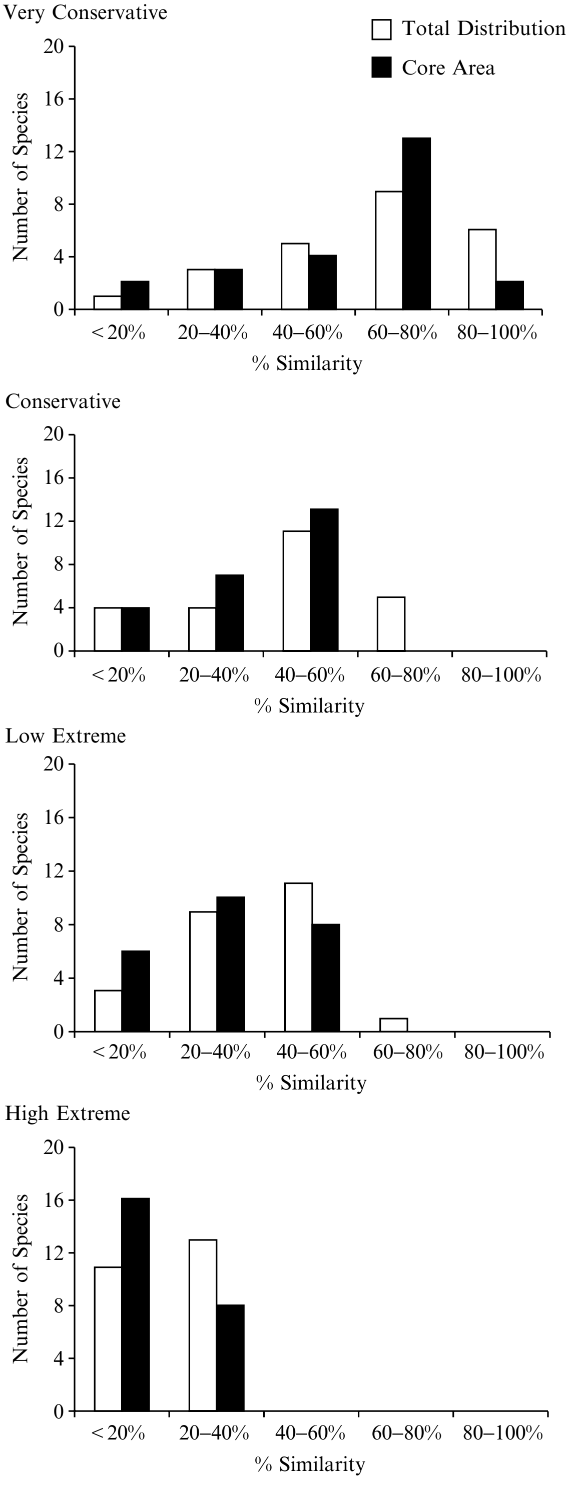

Fig. 6 (a)–(d) Percentage similarity indicates the proportion of grid cells present in each climate change scenario that are also present in the current potential climatic range of each species. Results are given for each species entire distribution (light bars) (light bars), and for those locations classified as core areas in each pair of scenarios (dark bars). Core areas are defined as locations where climatic parameters lie within the 2.5th to 97.5th percentiles of the species climatic envelopes.

Table 5 Characteristics of seven species that may be particularly vulnerable to climate change. The MAT range (mean annual temperature), precipitation ratio (highest:lowest mean annual rainfall), and the estimated seasonal changes in temperature and precipitation within the known distribution of each species are shown, as are characteristics of their life histories (Common & Waterhouse, 1981; Kitching *et al.*, 1999; Braby, 2000). Species designated as habitat specialists have less than four larval host plant species and are myrmecophytic

	MAT range (°C)	Precip ratio	2050 temp increase (°C)	2050 precip decrease (%)	Latitudinal range	Myrmecophile	Number of larval host plants	Habitat specialist	Poor dispersal	Geographically localised	Habitat destruction
Exometocea nycteris	2.8	3.3	0.5–2.5	0 to −30	3.5		?		✓		
Trapezites heteromacula	6.4	2.3	0.8–3.3	0 to −13	9.1		3		✓	✓	
Hypochrysops halyaetus	5.1	4.9	0.7–3.1	0 to −38	7.7	✓	4		✓		✓
H. piceata	0.7	1.0	0.9–3.5	0 to −22	0.1	✓	1	✓	✓	✓	✓
Jalmenus clementi	3.1	1.3	0.9–3.3	0 to −30	2.1	✓	3	✓	✓	✓	
J. lithochroa	3.3	2.9	0.9–2.8	0 to −19	3.4	✓	2	✓	✓	✓	✓
Nesolycaena urumelia	2.5	3.1	0.9–3.7	0 to −30	6.7		2			✓	

to less than 37% of the size of its current climatic range, while under the high extreme scenario, this species distribution may decrease in size by more than 90%. Less than 35% of areas suitable under the very conservative scenario coincide with areas that are currently suitable. Under the high extreme scenario, less than 7% of this species potential distribution is predicted to lie in locations that are currently climatically suitable. *Trapezites heteromacula* is restricted to north-east Queensland, where its distribution spans less than 10° latitude. Colonies are discrete and highly localised (Braby, 2000), and the larval food plant, *Lomandra*, is rarely found in large patches at any one location. Hence population density is low (Kitching *et al*., 1999), and the likelihood of this species shifting its distribution to compensate for habitat loss under climate change is poor.

Sources of uncertainty

Bioclimatic models do not represent forecasts of future distributions, but rather provide an indication of the potential magnitude of the impact climate change may have on these species distributions (Hill *et al*., 1999). Bioclimatic models remain the only method available to rapidly assess potential broadscale changes in the distributions of multiple species in response to a changing climate. However, the effects of global change on species distributions are unlikely to be as simple as bioclimatic models infer. Factors that may influence the reliability of our results can be placed into three categories: (a) limitations associated with BIOCLIM, (b) uncertainty in climate change scenarios, and (c) complex biotic interactions.

(a) Limitations associated with BIOCLIM Nix (1986) has outlined in detail the limitations and errors associated with BIOCLIM. These include errors associated with taxonomy, incorrect locations, and limitations of computer models. The Dunn & Dunn National Database of Australian Butterflies has attempted to control for errors associated with species' distributions by using up-to-date taxonomy lists, and by re-examining specimens that have undergone important taxonomic changes. However, there may still be errors in defining locations on specimen labels, and similarly, the current ranges of species may not yet be fully known.

The effectiveness of any model is also governed by its assumptions. Firstly, bioclimatic models assume that climate limits species distributions (Panetta & Mitchell, 1991a), hence only a species fundamental niche is modelled, while factors that determine the realised niche such as host plant availability, predators, and competitors are not considered. Secondly, the model assumes that there is genetic homogeneity in the response of a species to climate (Panetta & Mitchell, 1991a,b), and thirdly, that species have reached the limits of their current climatic range. The effectiveness of BIOCLIM has been questioned by some authors (see Walker & Cocks, 1991; Carpenter *et al*., 1993; Kriticos & Randall, 2001), primarily because the suitable range for each climatic variable is described as a rectilinear volume in Euclidean space. As a result, habitat suitability may not be predicted correctly. However, BIOCLIM remains a useful tool for studying potential changes in distributions and for identifying species on which to focus future field work. Further, at present, it is, to our knowledge, the most feasible program for studying the potential responses of a large number of species to climate change.

(b) Uncertainty in climate change scenarios As the level of resolution of climate change scenarios increases, so too does uncertainty. Naturally, results obtained from this study are applicable only for those scenarios used, and as yet it is uncertain how robust BIOCLIM estimations are to standard deviations of climate change scenarios. Future field studies will be necessary to determine whether trends hypothesised from this study have actually occurred.

Furthermore, it is largely unknown how temperature and precipitation changes estimated from global circulation models (GCMs) will translate into changes in the microclimate of species (e.g. see Kennedy, 1997). Bioclimatic models apply a uniform increase in temperature over each cell of the climatic grid, but undoubtedly, temperature changes estimated by GCMs will not translate into the same temperature changes within different microhabitats.

(c) Complex biotic interactions As climate changes, the ability of a species to take advantage of climatically suitable areas will depend upon a suite of factors not considered in bioclimatic models, such as competition and predation between existing species, and the potential impact of interactions with new species. The ability of species to shift their distributions will also depend upon their dispersal abilities and the distribution and quality of host plants (see Coviella & Trumble, 1999). Many Australian butterfly species (such as *Trapezites*) are unable to migrate, and the dispersal ability of groups such as the lycaenids are also believed to be limited (Kitching *et al*., 1999). Furthermore, the spatial structure of many butterfly populations is consistent with metapopulation theory, that is, populations are more likely to be present in habitat patches that are large and in close proximity to one another (Thomas & Hanski, 1997). Land clearance and habitat fragmentation due to human land use has already played a major role in the demise of many Australian butterfly species. Future fragmentation of habitat as a result of climate change may compound

existing problems and have further implications for dispersal success and the stability of the metapopulation structure. Distributions may also be affected if closely coupled phenologies of host plants and herbivores become desynchronised (e.g. see Dewar & Watt, 1992; Buse *et al*., 1998). Hence, in many cases, the distribution changes hypothesised in this study may represent best-case scenarios.

It is possible that some species may be able to adapt *in situ* rather than shift their distributions. Adaptations of British butterflies that now occur in warmer and drier regions throughout the world have been studied extensively (Pollard & Yates, 1993), and suggest that some species may respond in a number of ways, including changes in voltinism, dates of emergence, delayed maturation of eggs (Pollard & Yates, 1993), and the length-of-the-flight period (Brakefield, 1987; Pollard, 1991).

To gain a broader understanding of the potential responses of species to climate change, ongoing monitoring of vulnerable species is required. Compared to many countries in the Northern Hemisphere, Australia suffers a lack of peer-reviewed literature related to the potential responses of species to climate change. Studies such as this can help to identify areas in which we can focus our future research.

Acknowledgements

We thank Mike Poulsen for providing assistance with the DEM, Jennifer Crossley from CRU for supplying the climate change scenarios, and Andy Pitman for advice on climate modelling. Many thanks also to Caitlin Johns, Janet Lake, and Nigel Andrew for their helpful comments. Finally, we in are debt to all the amateur and professional butterfly collectors whose data we used, and to K and L. Dunn for compiling the National Database of Australian Butterflies.

References

ArcInfo V. 7.2 (1999) Environmental Systems Research. Institute, Inc, Redlands, CA.

ArcView V3.0 (1999) Environmental Systems Research. Institute, Inc, Redlands, CA.

AUS40.DEM (1999) Centre for Resource and Environmental Studies, Australian. National University, Canberra.

Ayres MP, Scriber JM (1994) Local adaptations to regional climates in *Papilio candaensis* (Lepidoptera: Papilionidae). *Ecological Monographs*, **64**, 465–482.

Bennett S, Brereton R, Mansergh I *et al.* (1991) *The Potential Effect of the Enhanced Greenhouse Climate Change on Selected Victorian Fauna*. Arthur Rylah Institute for Environmental Research, Technical Report Series No. 123, Scientific Publications and Biometrics Section, Department of Conservation and Environment, Kew.

Braby MF (2000) *Butterflies of Australia: Their Identification, Biology and Distribution*. CSIRO Publishing, Collingwood.

Brakefield P (1987) Geographical variability in and temperature effects on the phenology of *Maniola jurtina and Pyronia tithonus* (Lepidoptera: Satyrinae) in England and Wales, UK. *Ecological Entomology*, **12**, 139–148.

Busby JR (1991) BIOCLIM—a bioclimatic analysis and prediction system. *Plant Protection Quarterly*, **6**, 8–9.

Buse A, Dury SJ, Woodburn RJW *et al.* (1999) Effects of elevated temperature on multi-species interactions: the case of Pedunculate Oak, Winter Moth and Tits. *Functional Ecology*, **13** (Suppl. 1), 74–82.

Buse A, Good JEG (1996) Synchronization of larval emergence in winter moth (*Operophtera brumata* L.) and budburst in pedunculate oak (*Quercus robur* L.) under simulated climate change. *Ecological Entomology*, **21**, 335–343.

Buse A, Good JEG, Dury SJ *et al.* (1998) Effects of elevated temperature and carbon dioxide on the nutritional quality of leaves of oak (*Quercus robur* L.) as food for the winter moth (*Operophtera brumata* L.). *Functional Ecology*, **12**, 749–749.

Carpenter G, Gillison AN, Winter J (1993) DOMAIN: a flexible modelling procedure for mapping potential distributions of plants and animals. *Biodiversity and Conservation*, **2**, 667–680.

Casey TM (1993) Effects of temperature on foraging of caterpillars. In: *Caterpillars—Ecological and Evolutionary Constraints on Foraging* (eds Stamp NE, Casey TM), pp. 5–28. Chapman & Hall, London.

Common IFB, Waterhouse DF (1981) *Butterflies of Australia*. CSIRO Publications, East Melbourne, 682 pp.

Coviella CE, Trumble JT (1999) Effects of elevated atmospheric carbon dioxide on insect–plant interactions. *Conservation Biology*, **13**, 700–712.

Dawson WR (1992) Physiological responses of animals to higher temperatures. In: *Global Warming and Biological Diversity* (eds Peters RL, Lovejoy TE), pp. 138–158. Yale University, New Haven.

Dennis RLH (1993) *Butterflies and Climate Change*. Manchester University Press, Manchester, 302 pp.

Dewar RC, Watt AD (1992) Predicted changes in the synchrony of larval emergence and budburst under climatic warming. *Oecologia*, **89**, 557–559.

Drake VA (1994) The influence of weather and climate on agriculturally important insects: an Australian perspective. *Australian Journal of Agricultural Research*, **45**, 487–509.

Dunn KL, Dunn LD (1991) *Review of Australian Butterflies: Distribution, Life History and Taxonomy*, Vol. 1–4. Privately published.

Eeley HAC, Lawes MJ, Piper SE (1999) The influence of climate change on the distribution of indigenous forests in KwaZulu-Natal, South Africa. *Journal of Biogeography*, **26**, 595–617.

Ellis WN, Donner JH, Kuchlein JH (1997) Recent shifts in phenology of Microlepidoptera, related to climate change (Lepidoptera). *Entomologische Berichten Amsterdam*, **57**, 66–72.

Gilbert N (1984) Control of fecundity in *Pieris rapae* II. Differential effects of temperature. *Journal of Animal Ecology*, **53**, 589–597.

Hill JK, Thomas CD, Huntley B (1999) Climate and habitat availability determine 20th century changes in a butterfly's range margin. *Proceedings of the Royal Society of London B*, **266**, 1197–1206.

Houlder D, Hutchinson M, Nix H *et al.* (1999) *ANUCLIM Version 5.0 User Guide*. Centre for Resource and Environmental Studies, Australian National University, Canberra.

Hughes L (2000) Biological consequences of global warming: is the signal already apparent? *Trends in Ecology and Evolution*, **15**, 56–61.

Hughes L, Cawsey EM, Westoby M (1996) Climatic range sizes of *Eucalyptus* species in relation to future climate change. *Global Ecology and Biogeography Letters*, **5**, 23–29.

Hulme M, Sheard N (1999) *Climate Change Scenarios for Australia*. Climatic Research Unit, Norwich, UK.

Intergovernmental Panel on Climate Change (IPCC) (2001) *Climate Change 2001: the Scientific Basis WGI Third Assessment Report*. Cambridge University Press, Cambridge.

Jones RE, Hart JR, Bull GD (1982) Temperature, size and egg production in the Cabbage Butterfly, *Pieris rapae* L. *Australian Journal of Zoology*, **30**, 223–232.

Kennedy AD (1997) Bridging the gap between general circulation model (GCM) output and biological microenvironments. *International Journal of Biometeorology*, **40**, 119–122.

Kitching RL, Scheermeyer E, Jones RE *et al.* (1999) *Biology of Australian Butterflies*. Monographs on Australian Lepidoptera, Vol. 6. CSIRO Publishing, Collingwood, 395 pp.

Kristiansen G (1993) *Biological Effects of Climate Change: An Introduction to the Field and Survey of Current Research*. Global Change & Terrestrial Ecosystems, Centre for International Climate and Energy Research, Oslo, 190 pp.

Kriticos DJ, Randall RP (2001) A comparison of systems to analyse potential weed distributions. In: *Weed Risk Assessment* (eds Groves RH, Panetta FD, Virtue JG), pp. 61–79. CSIRO Publishing, Collingwood.

Kuchlein JH, Ellis WN (1997) Climate-induced changes in the microlepidoptera fauna of the Netherlands and the implications for nature conservation. *Journal of Insect Conservation*, **1**, 78–80.

Liu S, Zhang G, Zhu J (1995) Influence of temperature variations on rate of development in insects: analysis of case studies from entomological literature. *Annals of the Entomological Society of America*, **88**, 107–119.

Mann ME, Bradley RS, Hughes MK (1999) Northern hemisphere temperatures during the past millennium: Inferences, uncertainties, and limitations. *Geophysical Research Letters*, **26**, 759–762.

Nicholls N, Lavery B (1992) Rainfall trends during the twentieth century. *International Journal of Climate*, **12**, 153–163.

Nix H (1986) *A Biogeographic Analysis of Australian Elapid Snakes*, Australian Flora and Fauna Series No. 7 (ed. Longmore R), Bureau of Flora and Fauna, Canberra, Australian Government Publishing Service, Canberra, 15 pp.

Panetta FD, Mitchell ND (1991a) Homoclime analysis and the prediction of weediness. *Weed Research*, **31**, 273–284.

Panetta FD, Mitchell ND (1991b) Bioclimatic prediction of the potential distributions of some weed species prohibited entry to New Zealand. *New Zealand Journal of Agricultural Research*, **34**, 341–350.

Parmesan C (1996) Climate and species' range. *Nature*, **382**, 765–766.

Parmesan C, Ryrholm N, Stefanescu C *et al.* (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579–583.

Peters RL, Darling JDS (1985) The greenhouse effect and nature reserves. *Bioscience*, **35**, 707–717.

Pollard E (1988) Temperature, rainfall and butterfly numbers. *Journal of Applied Ecology*, **25**, 819–828.

Pollard E (1991) Changes in the flight period of the Hedge Brown Butterfly *Pyronia tithonus* during range expansion. *Journal of Animal Ecology*, **60**, 737–748.

Pollard E, Moss D, Yates TJ (1995) Population trends of common British butterflies at monitored sites. *Journal of Applied Ecology*, **32**, 9–16.

Pollard E, Rothery P, Yates TJ (1996) Annual growth rates in newly established populations of the butterfly *Pararge aegeria*. *Ecological Entomology*, **21**, 365–369.

Pollard E, Yates TJ (1993) *Monitoring Butterflies for Ecology and Conservation*. Chapman & Hall, London, 274 pp.

Roy DB, Sparks TH (2000) Phenology of British butterflies and climate change. *Global Change Biology*, **6**, 407–416.

Salinger MJ, Allan R, Bindoff N *et al.* (1996) Observed variability and change in climate and sea level in Australia, New Zealand and the south Pacific. In: *Greenhouse: Coping with Climate Change* (eds Bouma WJ, Pearman GI, Manning MR), pp. 100–107. CSIRO Publishing, Collingwood.

Salinger MJ, Stigter CJ, Das HP (2000) Agrometeorological adaptation strategies to increasing variability and climate change. *Agricultural and Forest Meteorology*, **103**, 167–184.

Scriber JM, Lederhouse RC (1983) Temperature as a factor in the development and feeding ecology of tiger swallowtail caterpillars, *Papilio glaucus* (Lepidoptera). *Oikos*, **40**, 95–102.

Sparks TH, Yates TJ (1997) The effect of spring temperature on the appearance dates of British butterflies 1883–1993. *Ecography*, **20**, 368–374.

SPSS v 8.0.2 (1998) SPSS Inc., Chicago.

Stamp NE, Bowers MD (1994) Effect of temperature and leaf age on growth versus moulting time of a generalist caterpillar fed plantain (*Plantago lanceolata*). *Ecological Entomology*, **19**, 199–206.

Taylor MFG (1988) Field measurement of the dependence of life history on plant nitrogen and temperature for a herbivorous moth. *Journal of Animal Ecology*, **57**, 873–891.

Thomas CD, Hanski I (1997) Butterfly metapopulations. In: *Metapopulation Biology: Ecology, Genetics and Evolution* (eds Hanski I, Gilpin ME), pp. 359–388. Academic Press, San Diego.

Virtanen R, Neuvonen S (1999) Climate change and macrolepidopteran biodiversity in Finland. *Chemosphere: Global Chance Science*, **1**, 439–448.

Walker PA, Cocks KD (1991) HABITAT: a procedure for modelling a disjoint environmental envelope for a plant or animal species. *Global Ecology and Biogeography Letters*, **1**, 108–118.

Wickman P (1988) Dynamics of mate-searching behaviour in a hilltopping butterfly, *Lasiommata megeria* (L.): the effects of weather and male density. *Zoological Journal of the Linnean Society*, **93**, 357–377.