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Ecological biogeography of species of *Gelonus*, *Acantholybas* and *Amorbus* in Australia

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Abstract Geographic ranges and host plants of 10 species of Australian coreid, *Gelonus tasmanicus*, *Acantholybas brunneus*, *Amorbus alternatus*, *Am. atomarius*, *Am. biguttatus*, *Am. bispinus*, *Am. obscuricornis*, *Am. rhombifer*, *Am. robustus* and *Am. rubiginosus*, were summarized using data from specimen collection labels and sampling. One process (CLIMEX) and two correlative range-modelling programs (BIOCLIM and DOMAIN) were used to infer the bioclimatic profiles of each species. By inference from the maximum range predictions made by CLIMEX, the suggestion that *G. tasmanicus*, *Am. atomarius* and *Am. obscuricornis* are temperate species was supported. Similarly, the suggestions that *Ac. brunneus* was a subtropical species and *Am. biguttatus* and *Am. rhombifer* are predominantly tropical species were supported. That *Am. alternatus*, *Am. robustus* and *Am. rubiginosus* are apparently ubiquitous species was supported. Comparison of the bioclimatic profiles of the habitats of *G. tasmanicus* and *Am. obscuricornis* within Tasmania using BIOCLIM supported information available in the published literature, that is, that *G. tasmanicus* is better suited to sites at higher elevations than *Am. obscuricornis*. In addition, the suggestion that the regions of high *Amorbus* species endemism should overlap with regions of high eucalypt species endemism was also supported. This finding is taken as evidence that the evolutionary radiation of *Amorbus* has followed that of the eucalypts. Using these models we have obtained preliminary insights into the biology of each species and the environmental characteristics of their preferred climatic envelope. This is an achievement that might never have been attained through concentrated study given that these insects can vary from being rare to, at best, locally common in occurrence.

Key words: *Eucalyptus*, habitat preferences, herbivorous insects, host-specificity, speciation.

INTRODUCTION

Ecological biogeography attempts to explain the suitability of disparate geographical regions to particular organisms through an understanding of the physical and climatic requirements of the species in question (Cranston & Naumann 1991). Climate, in particular temperature, is generally considered to be the major determinant influencing a species' geographical range (Kukal *et al.* 1991; Jeffree & Jeffree 1994). Temperature can also influence local adaptation within a species across different regions of its range (Baldwin & Dingle 1986; Ayres 1991; Ayres & Scriber 1994).

Considering the size of the Australian insect fauna there have been comparatively few (e.g. McQuillan & Ek 1996; Yonow & Sutherst 1998) attempts to relate the ranges of endemic insects to recorded environmental data. Typically, other techniques have been employed to comment upon a species' climatic preferences (Colless 1980; Allsopp 1995). Davidson (1934, 1935, 1936) pioneered this area in Australia by using temperature and moisture to delimit bioclimatic zones and related these to insect ecology but did not consider any particular species.

In order to infer the physical and climatic requirements of a species, and thereby compare these requirements with those of another species, information that enables the geographical range of the species in question to be determined is needed. Not surprisingly, the collection labels of museum specimens can contain just such information as well as a considerable amount of ecological information. This is especially true when the specimens come from a variety of localities, hosts and/or times of year. Bioclimatic modelling packages offer the potential to infer the bioclimatic requirements of a species and predict the maximum geographical range of a species without the need for laboratory developmental assays or exten-

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sive surveys, respectively. For example, McQuillan and Ek (1996) used the climatic analysis software package BIOCLIM to summarize the environmental parameters characteristic of Tasmanian collection locations of the Ptunarra brown butterfly, *Oreixenica ptunarra*. These authors found that *O. ptunarra* occurred in habitats that differed notably with respect to annual rainfall but not temperature, in particular annual temperature range. The existence of a longitudinal cline, probably related to increased efficiency of thermoregulation for adult activity in more marginal habitats, was demonstrated (McQuillan & Ek 1996).

For wholly herbivorous species, the availability of suitable host plants is an a priori requirement for their presence within a given habitat. This relationship is, perhaps not unexpectedly, not reciprocal. That herbivore ranges are often less extensive than those of their host plants is well documented (MacLean 1983; McClure 1989; Zalucki *et al.* 1994). MacLean (1983) proposed that differences in the development time of the host (specifically reproductive structures) and its insect herbivore could effectively exclude the latter from regions of the plants' range (demonstrated by Pearsall 1950). However, this interaction may not be as exclusive for those insect–plant associations where the herbivore feeds on vegetative structures. Generally, the vegetative structures of the Australian flora are ever present, that is, most species are evergreen.

Insects belonging to the family Coreidae (within the suborder Heteroptera, the 'true bugs' (see Schuh & Slater 1995)), are particularly interesting study organisms, especially their life histories (Maschwitz *et al.* 1987) and mating behaviours (Mitchell 1980; Eberhard 1998). However, in Australia the majority of species are of no commercial significance and as a result have received very little scientific attention. All members of the subfamily Coreinae are phytophagous and feed by suction through hinged stylets that are contained within a rostrate labium (i.e. they have elongate mouthparts). The stylets are inserted into the plant tissues to remove liquid nutrients. In addition, coreids possess metathoracic scent glands that release pungent odours when the insect is alarmed. At present the genus *Gelonus* is considered monospecific and is included in the tribe Amorbini (but see Steinbauer 1995). *Gelonus tasmanicus* adults are approximately 14–15 mm long, have a less robust body shape than either *Acantholybas* or *Amorbus*, are mostly black in colour when viewed dorsally and the males lack swollen hind femora (Steinbauer 1995). In Tasmania, *G. tasmanicus* appears specific for eucalypts belonging to the gum and ash groups (Steinbauer 1997b). The genus *Acantholybas* (one of more than 19 genera in the tribe Colpurini) presently consists of four species (Steinbauer & Clarke 1996). Adult *Acantholybas* range in length from 8 to 12 mm, are dorso-ventrally pronounced, brown to dark brown in colour when viewed dorsally and the males lack swollen hind femora (Steinbauer 1995; Steinbauer & Clarke 1996). The presently available evidence suggests that species of *Acantholybas* are polyphagous (i.e. there are collection records from host plant species belonging to a number of families (Steinbauer & Clarke 1996)). The genus *Amorbus* is the most speciose of the genera considered here. It is presently thought to contain in excess of 20 species (Steinbauer 1995). Species of *Amorbus* range in length from 15 to 24 mm, the margins of the abdomen are laterally expanded (especially in the females), yellow to brown-red in colour when viewed dorsally and the males have swollen hind femora and spined tibiae (Steinbauer 1995). In Tasmania, *Am. obscuricornis* inhabits dry to wet sclerophyll forest and, possibly as a consequence, is host specific for eucalypts belonging to the gum, ash and peppermint groups, that is, the entire range of eucalypt groups in that state (Steinbauer 1997b). Both *G. tasmanicus* and *Am. obscuricornis* are univoltine and overwinter as adults, relying on stored lipids (Steinbauer 1997a, 1998). Steinbauer *et al.* (1998) reported that *Am. obscuricornis* selected between apical shoots of eucalypt hosts based on their nutritional quality, which is autocorrelated with their vigour. This suggests that environmental factors (e.g. rainfall and fire) that influence eucalypt shoot growth could have a significant effect on the population ecology of *Amorbus* species (Steinbauer 1999).

It was our intention to map the known ranges of these coreid species and to compile a list of possible host plants. Then, we harnessed the 'latent potential' (*sensu* Nix 1986) of this information to predict the maximum Australian ranges of the species using CLIMEX and DOMAIN as well as the climatic characteristics of their habitats using BIOCLIM. Our objectives were to: (i) infer the climatic requirements of each species (using output from different sources) and predict their maximum geographical range with a view to re-examining statements concerning habitat preferences in Steinbauer (1995); (ii) consider the influence of insect host specificity to geographical range; and, to a lesser extent (iii) compare the predictions of the models used.

We use the present study as an example of the more general principle that major ecological insights about relatively rare species can be derived by applying distribution models to data from previous collections.

METHODS

Specimen collections

Institutions' collections of coreids belonging to the three genera from around Australia, and internationally in some instances, were examined and details from specimen labels recorded. In addition to collection specimens, some sampling in Tasmania, Victoria, the Northern Territory (M. J. Steinbauer) and New South Wales (M. J. Steinbauer & R. Cant) was also undertaken. Entire collection locality details for the specimens (approximately 1793 insects) used to compile the data employed herein are given in Steinbauer (1995). Data from nymphal specimens were not used as these stages cannot be identified to species. Within *Acantholybas* and *Amorbus*, only named species endemic to Australia and Papua New Guinea are considered.

Geocoding

Grid references were obtained for collection localities using the Master Names File (MNF) of Australian localities (compiled by the Australian Surveying & Land Information Group (AUSLIG)). When precise grid locations were not given on the specimen label, we attempted to infer the closest grid reference possible using the MNF. Where necessary this was supplemented with examination of 1:100 000 or 1:250 000 topographic maps. For each species, only unique instances of capture (i.e. date, host and/or collector) were used to compile lists of collection grid references (i.e. multiple specimen records were not used). The number of collection localities used for each species considered in the predictions is given in the Results section. We suggest that the process by which we compiled our collection locality data should be considered 'haphazard', that is, our data were gathered using a process that does not guarantee that random selection was used but it was a process that is thought to have avoided serious bias. Species' collection locations were mapped using MapInfo.

BIOCLIM version 1.0

Unlike process-modelling programs, correlative range-modelling programs (i.e. BIOCLIM (see Nix 1986; Podger *et al.* 1990; Williams 1991) and DOMAIN) use collection locality records as surrogates for experimentally derived organism performance parameters (Carpenter *et al.* 1993). BIOCLIM uses a set of continuous mathematical surfaces that are modelled from long-term mean monthly temperature and precipitation across Australia. BIOCLIM can estimate up to 16 indices from these surfaces for any location defined by latitude, longitude and elevation, for example a grid location for one or more specimens (Podger *et al.* 1990). Because few of the coreid specimen labels examined provided the elevation of the collection location, we used the digital elevation model to estimate height ASL for each grid reference. A key to the nine BIOCLIM bioclimatic index abbreviations used herein is given in Appendix I.

The Australia-wide grid references were employed to model the bioclimatic parameters of each species' habitat using BIOCLIM. In addition, we compared the experimentally derived developmental data obtained for *G. tasmanicus* and *Am. obscuricornis* with the climatic characteristics obtained using BIOCLIM for the habitats where both species had been collected in Tasmania. This approach was also employed because the topography in Tasmania is often at a much finer scale than at many of the mainland locations where these two species have been recorded. Relatedly, the Tasmanian climate is considered temperate maritime with only a small continental effect, unlike mainland Australia (Anonymous 1993).

CLIMEX version 1.1 for Windows 95

CLIMEX (see Sutherst & Maywald 1985; Sutherst *et al.* 1995, 1998; Yonow & Sutherst 1998) is a process simulation model that allows the estimation of a species' geographical distribution and relative abundance as determined by climate. CLIMEX can be applied to species in two ways. Parameter values describing the species' responses to temperature and moisture can either be inferred from the geographical distribution or set using available biological data. Using either type of data, an annual population growth index and four stress indices (cold, hot, wet and dry) are estimated. The growth and stress indices are combined into an ecoclimatic index (EI) to give an overall estimate of the favourableness of the location for permanent occupation by a species. The CLIMEX meteorological database contains data for approximately 700 locations in Australia. The database consists of long-term monthly averages that have undergone considerable smoothing of daily values. Therefore, CLIMEX values cannot be directly equated with either laboratory or instantaneous field values. The locations from which meteorological data are taken are not uniformly distributed across the continent. A digital elevation model (see also BIOCLIM) is used to generate a long-term average climate surface for Australia on a 50-km^2 grid (Yonow & Sutherst 1998). A key to the parameter values of CLIMEX is presented in Appendix II.

We used CLIMEX to infer parameter values for each species based on the collection locality records for Australia (see previous comments). We employed an iterative approach to each species in order to achieve the best fit between the locality records and the model prediction. We have only presented the CLIMEX predictions concerning those locations that have a favourable environment for each species.

DOMAIN version 1.3 for Windows

DOMAIN (after Carpenter *et al.* 1993) uses a point-to-point similarity metric (ultimately the climatic similarity metric (S)) to assign a classification value to a potential collection locality based on the proximity in environmental space of the most similar collection locality record and thereby defines geographical ranges. DOMAIN does not define discrete boundaries for the climate envelope. All potential collection localities are assigned similarity values and user-defined thresholds or contour intervals determine the actual ranges mapped. For example, a threshold of $S = 0.90$ selects points with an average variation in climatic values from a known occurrence site of no more than 10% of the range.

Five climatic layers (mean annual rainfall, variation in rainfall, rainfall of the driest quarter, minimum

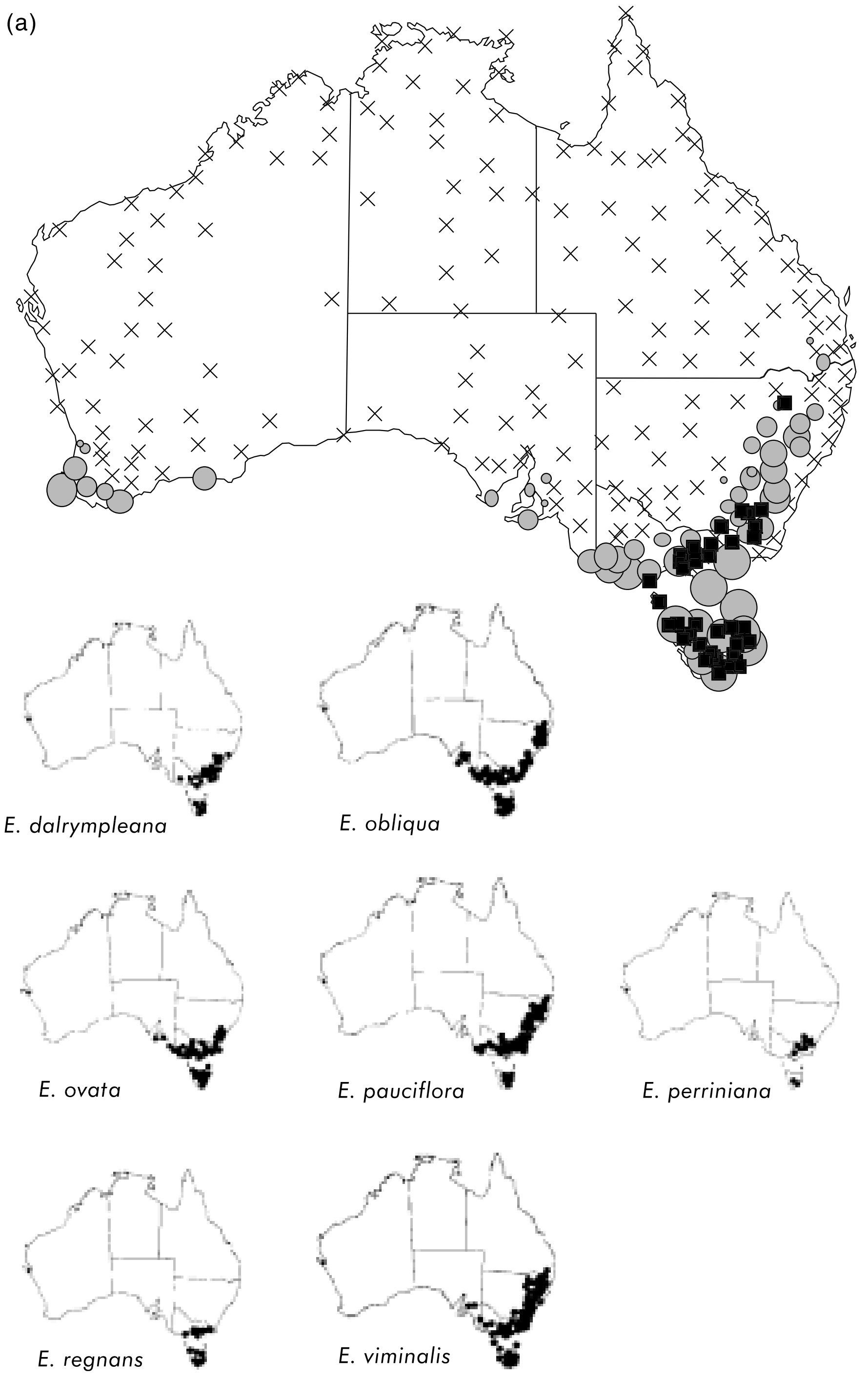


Fig. 1. Collection localities and predicted maximum ranges of *Gelonus tasmanicus* in Australia. (a) Collection locality records (■) with EcoClimatic Indices (EI) (shaded circles with size indicating location suitability, larger circles for more favourable locations; ×, unsuitable location (EI = 0)) from CLIMEX prediction superimposed. For the sake of figure simplicity, the CLIMEX prediction utilizes 228 of the total 675 meteorological locations for which climatic data are available. Ranges of selected eucalypt hosts, reproduced from Chippendale (1988), shown below map (complete list given in Table 1). (b) Collection locality records (●) superimposed on DOMAIN prediction (shade indicates regional climatic similarity: light grey, S = 85–90%; grey, S = 91–95%; dark grey, S = 96–100%).

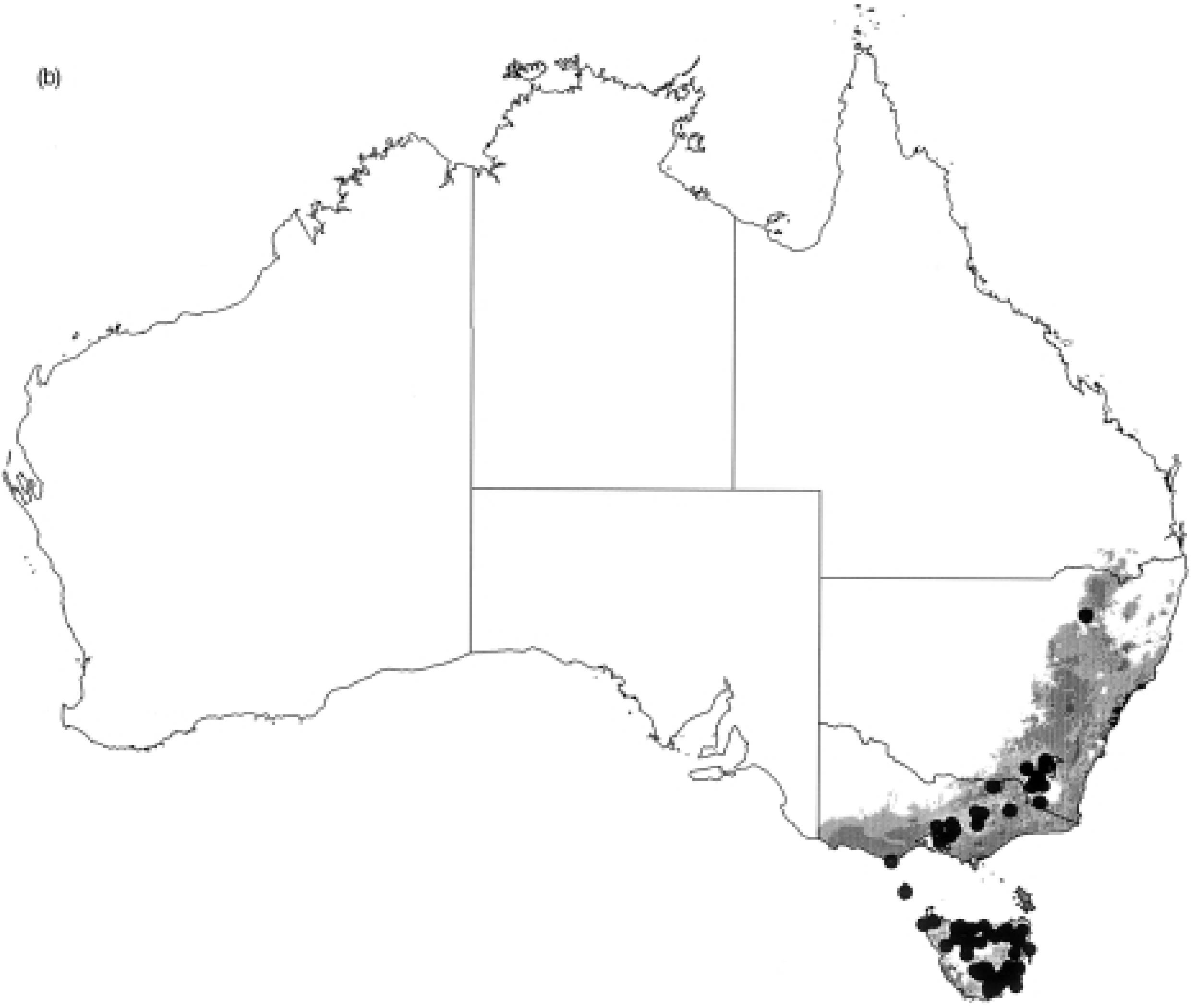


Fig. 1. continued

and maximum temperature) and one physical layer (elevation) were employed to define the DOMAIN similarity values relative to the insect collection localities. The three user-defined DOMAIN climatic similarities (*S*) we used were $S = 85–90$, 91–95 and $S = 96–100\%$.

RESULTS

Australia-wide coreid and host plant distributions, CLIMEX/DOMAIN predictions and bioclim results

Gelonus tasmanicus

This species' apparent geographical range encompasses south-east Australia (94 unique collection records; Fig. 1a,b). The apparent range of *G. tasmanicus* is typical of other insects common to Tasmania and the Australian mainland, for example *Mnesampela heliochrysa* (McQuillan 1985). On the Australian mainland the species appears predominantly restricted to inland and higher altitude regions of the Great Dividing Range and Snowy Mountains. There is a high degree of similarity between the distribution of *G. tasmanicus* and the distributions of the known hosts (Fig. 1a; Table 1). The maximum range predicted by CLIMEX supports the proposition, based on the collection records, that this is a temperate species. The use of the hot-wet stress interaction in the CLIMEX prediction (Table 2) is questionable, but provided the means to match the observed distribution most closely. The largest areas of high climatic similarity, as predicted by DOMAIN, to the collection localities occur in the eastern half of Tasmania (Fig. 1b). The Australia-wide bioclimatic estimates obtained for this species using BIOCLIM are typical of temperate regions and are of similar magnitude to the developmental temperature parameters used in the CLIMEX prediction (Table 3).

Acantholybas brunneus

The only Australian host record for this species is a grass (six unique collection records; Fig. 2a,b, Table 1). Consequently, we cannot bring any additional insight to our predictions other than that provided by the collection localities. In order to model the maximum range of this species using CLIMEX, we began with the temperate template provided in the program. We increased the values for DV0 and SM0 that are the defaults provided in the temperate template. In addition, we altered the parameters that dictate the accumulation of cold stress (Table 2). In this way we obtained a good match between the collection records and the possible maximum range for the species (Fig. 2a). The DOMAIN predicted distribution for this species is very restricted, with no regions where $S > 95\%$, and is predominantly centred around the collection localities (Fig. 2b). The collection localities for *Ac. brunneus* are characterized by high annual rainfall and mild temperatures according to BIOCLIM (Table 3).

Amorbus alternatus

Many of the collection records for *Am. alternatus* derive from semi-arid and arid regions (54 unique collection records; Fig. 3a,b). The distributions of the few eucalypt species recorded as being associated with this species do not correlate with the insect's apparent region of endemism. This suggests that *Am. alternatus* feeds upon other eucalypt species in addition to those cited. The CLIMEX parameter values (Table 2) reflect the wide range of habitats encompassed by this species' collection records. The resulting CLIMEX model would allow the species to exist almost Australia-wide, with

Table 1. Collection periods and host plant records for species of *Gelonus*, *Acantholybas* and *Amorbus*

Species	Collection period	Host plants
G. tasmanicus	September to May	*Eucalyptus dalrympleana*, *E. delegatensis*, *E. globulus*, *E. obliqua*, *E. ovata*, *E. pauciflora*, *E. perriniana*, *E. regnans*, *E. subcrenulata* and *E. viminalis* (also recorded on plantation *E. nitens* in Tasmania)
Ac. brunneus	March	Recorded on Gramineae in NSW (reared on *Yuccoides beshorneria* in New Zealand)
Am. alternatus	All months	*Eucalyptus acmenioides* (Kumar 1966), *E. blakelyi, E. drepanophylla* (Kumar 1966) and plantation *E. grandis* in Victoria
Am. atomarius	August to January, March to April & June	*Eucalyptus* sp.
Am. biguttatus	December to June	*Eucalyptus camaldulensis* and *E. miniata* (also collected 'sweeping mangroves' in the Northern Territory)
Am. bispinus	September to November & January to February	*Eucalyptus marginata*
Am. obscuricornis	September to May	*Corymbia maculata*,* *Eucalyptus amygdalina*, *E. dalrympleana*, *E. delegatensis*, *E. dives*, *E. fastigata*, *E. globulus*, *E. macrorhyncha*, *E. ovata*, *E. pauciflora*, *E. perriniana*, *E. pulchella*, *E. risdonii*, *E. rossii*, *E. stellulata*, *E. subcrenulata* and *E. viminalis* (also recorded on *Angophora* sp. in New South Wales, cultivated *E. globulus* in South Australia and plantation *E. nitens* in Tasmania)
Am. rhombifer	All months	*Angophora subvelutina*, *Eucalyptus amplifolia* and *E. microcorys* (Kumar 1966)
Am. robustus	August to June	*Eucalyptus albens*, *E. crebra*, *E. melliodora* and *E. microtheca* (also recorded on Ironbark in Queensland, i.e. a *Eucalyptus* sp. belonging to the series Siderophloiae, plantation *E. grandis* in Victoria and plantation *Corymbia maculata* and *Eucalyptus dunnii* in New South Wales)
Am. rubiginosus	September to June	*Angophora hispida*, *Corymbia maculata*,* *Eucalyptus acmenioides* (Kumar 1966), *E. blakelyi*, *E. bridgesiana*, *E. camaldulensis*, *E. cinerea*, *E. dives*, *E. fastigata*, *E. gamophylla*, *E. globulus* ssp. *bicostata*, *E. leucoxylon*, *E. macrorhyncha*, *E. melliodora*, *E. microcarpa*, *E. pilularis*, *E. sideroxylon* and *E. tetragona* (also recorded on Mallee in Western Australia, plantation *E. globulus* in New South Wales, plantation *E. camphora* hybrid in New South Wales, plantation *E. grandis* in Victoria, plantation *E. nitens* in New South Wales (Stone *et al.* 1998) and plantation *Corymbia maculata*, *Eucalyptus dunnii*, *E. microcorys*, *E. pilularis* (see also Moore 1972) and *E. saligna* in New South Wales)

Tree subspecies identities considered synonymous with species identity unless otherwise stated; *Ac. brunneus* is an introduced species in New Zealand (Steinbauer & Clarke 1996). **Corymbia maculata* does not occur naturally in the Australian Capital Territory, which draws into question the identity of the tree species as given by the specimens' collectors.

the exceptions of most of Tasmania, the Australian Alps and some desert regions of Western Australia (Fig. 3a). The absence of collection records for the species from much of Western Australia presents an interesting disparity with both the CLIMEX and DOMAIN predicted ranges. Whether *Am. alternatus* occurs in Western Australia can only be determined by specific sampling. The DOMAIN predicted distribution is divided into three

Table 2. CLIMEX parameter values giving the best visual fit to the distributions of species of *Gelonus*, *Acantholybas* and *Amorbus* in Australia

Parameter group and value	*G. tasmanicus*	*Ac. brunneus*	*Am. alternatus*	*Am. atomarius*	*Am. biguttatus*	*Am. bispinus*	*Am. obscuricornis*	*Am. rhombifer*	*Am. robustus*	*Am. rubiginosus*
Temperature index										
DV0 (°C)	10.0*	12.0	10.0	12.0	15.0	10.0	12.0*	12.0	15.0	12.0
DV1 (°C)	12.0	15.0	20.0	15.0	25.0	15.0	16.0	22.0	25.0	20.0
DV2 (°C)	24.0	24.0	30.0	24.0	33.0	25.0	24.0	35.0	35.0	32.0
DV3 (°C)	28.0	30.0	38.0	30.0	36.0	30.0	28.0	38.0	38.0	36.0
PDD	0	0	0	0	0	0	400	0	0	0
Moisture index										
SM0	0.2	0.4	0.06	0.2	0.25	0.15	0.2	0.1	0.05	0.05
SM1	0.4	0.6	0.1	0.4	0.8	0.4	0.4	0.3	0.2	0.1
SM2	1.8	1.5	0.8	1	1.9	1.2	1.8	1.8	1.5	1.3
SM3	2	2	1	1.5	2	1.5	2	2	2	2
Cold stress										
TTCS	0	0	2	0	0	2	0	2	2	0
THCS	0	0	0.2	0	0	0.2	0	0.1	0.02	0
DTCS	0	23	15	15	25	20	0	20	15	10
DHCS	0	0.00075	0.001	0.00015	0.0015	0.0006	0	0.0003	0.00015	0.0003
Heat stress										
TTHS (°C)	28.0	30.0	38.0	30.0	36.0	30.0	28.0	38.0	38.0	36.0
THHS	0.0007	0.005	0.005	0.01	0.01	0.002	0.0007	0.01	0.001	0.0008
DTHS	0	0	0	0	0	0	0	0	0	0
DHHS	0	0	0	0	0	0	0	0	0	0
Dry stress										
SMDS	0.2	0.4	0.06	0.2	0.25	0.15	0.2	0.1	0.05	0.05
HDS	0.03	0.008	0.005	0.008	0.005	0.005	0.03	0.01	0.0075	0.01
Wet stress										
SMWS	2	2	1.0	1.5	0	1.5	2	2	2	2
HWS	0.002	0.002	0.003	0.005	0	0.002	0.002	0.005	0.002	0.01
Hot-wet stress										
TTHW (°C)	20.0	–	–	–	–	21.0	–	–	–	–
MTHW	0.325	–	–	–	–	0.4	–	–	–	–
PHW	0.075	–	–	–	–	0.08	–	–	–	–

Key to parameter values given in Appendix II. *Based on developmental threshold values given in Steinbauer (1997a). See comments in Results section.

Table 3. Bioclimatic data from BIOCLIM predictions based on collection records of species of *Gelonus*, *Acantholybas* and *Amorbus* across Australia

Species	MAT	minTCM	maxTHM	Range	MTCQ	MTWQ	MTHQ	MTDQ	AR
G. tasmanicus	13.1	3.9	23.5	19.6	8.9	11.2	17.4	16.7	820
Ac. brunneus	19.8	7.7	29.0	21.3	14.8	23.9	24.0	15.8	1255
Am. alternatus	21.4	7.8	33.6	25.7	15.4	24.0	26.7	18.6	594
Am. atomarius	19.0	5.7	29.9	24.2	13.5	23.3	24.0	14.3	785
Am. biguttatus	25.6	15.5	33.2	17.6	22.3	27.5	28.2	22.6	1730
Am. bispinus	17.3	7.9	29.2	21.2	13.0	13.3	22.2	22.1	920
Am. obscuricornis	13.7	4.0	24.0	20.0	9.4	13.0	18.0	16.1	754
Am. rhombifer	20.9	9.5	30.0	20.6	16.2	24.0	24.9	17.8	1136
Am. robustus	22.5	9.6	33.0	23.4	17.2	26.2	27.0	18.8	855
Am. rubiginosus	18.8	6.5	30.0	23.5	13.5	20.3	23.8	17.3	836

Key to bioclimatic index abbreviations given in Appendix I.

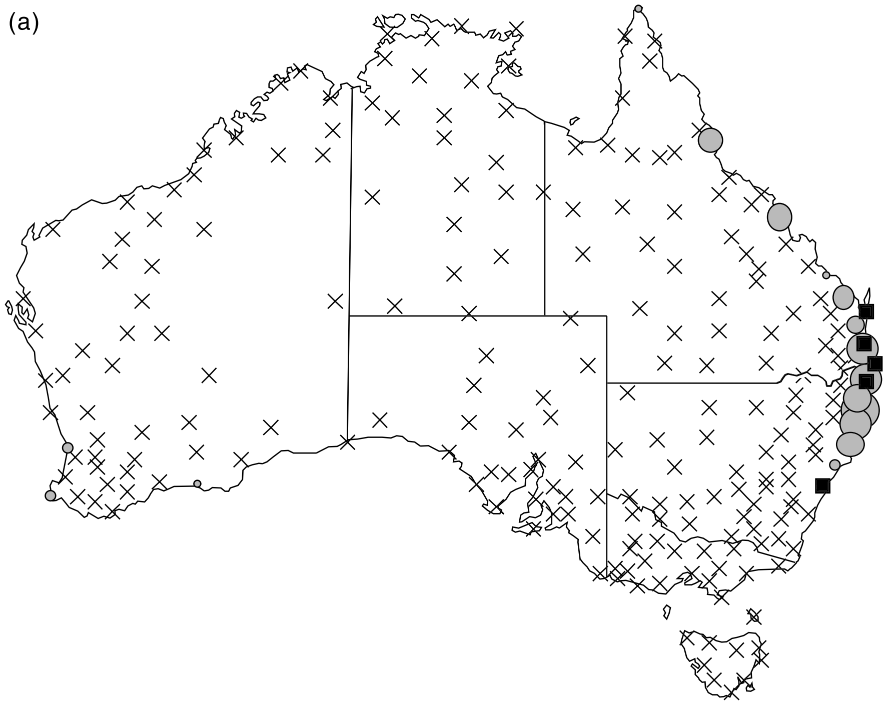
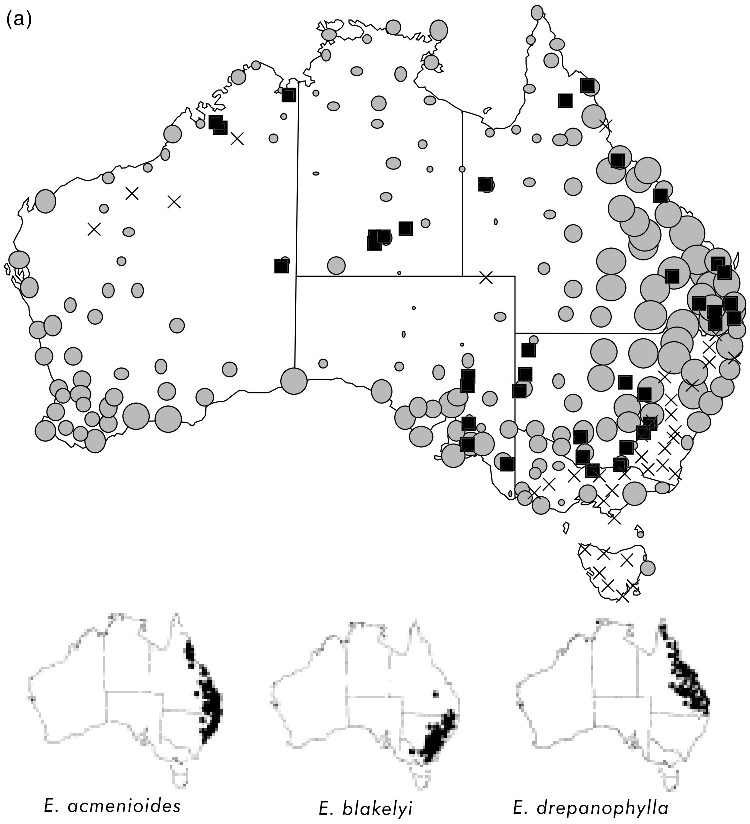


Fig. 2. Collection localities and predicted maximum ranges of *Acantholybas brunneus* in Australia. (a) Collection locality records (■) with EcoClimatic Indices (EI) (see Fig. 1 caption for explanation) from CLIMEX prediction superimposed. (b) Collection locality records (●) superimposed on DOMAIN prediction (see Fig. 1 caption for explanation).



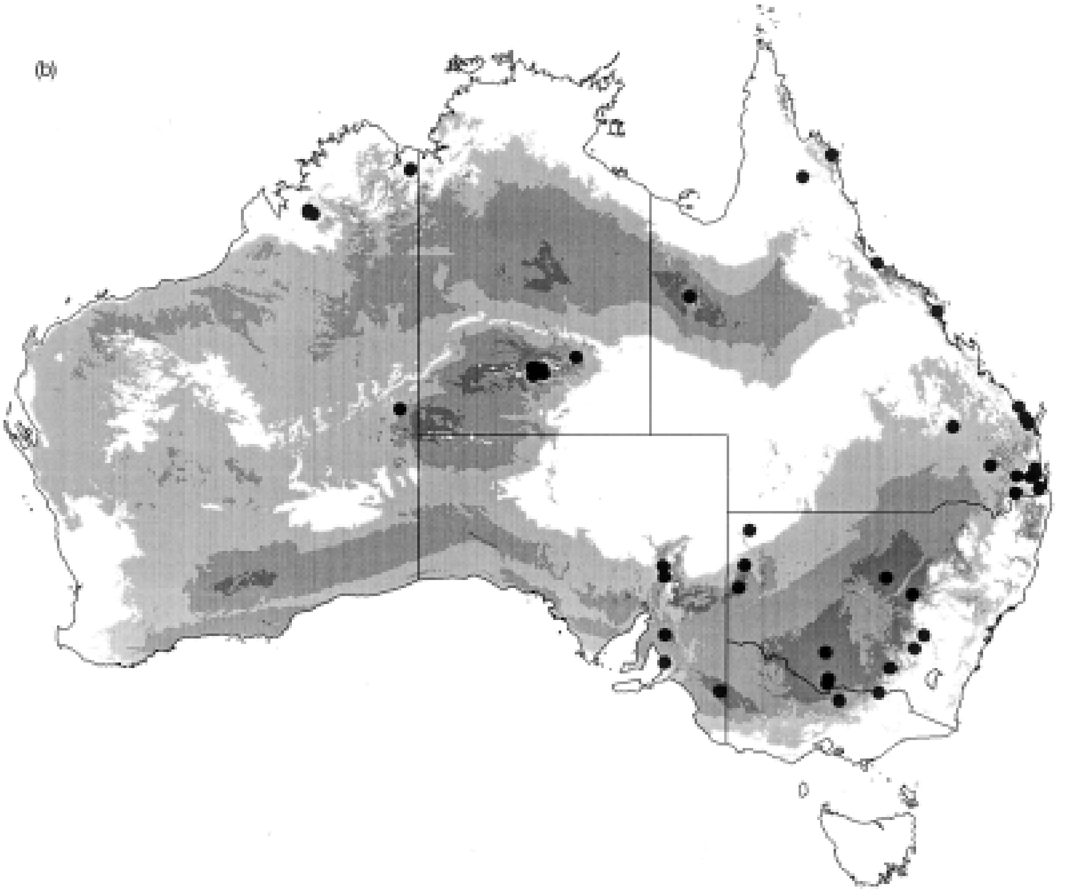


Fig. 3. Collection localities and predicted maximum ranges of *Amorbus alternatus* in Australia. (a) Collection locality records (■) with EcoClimatic Indices (EI) (see Fig. 1 caption for explanation) from CLIMEX prediction superimposed. Ranges of eucalypt hosts, reproduced from Chippendale (1988), shown below map. (b) Collection locality records (●) superimposed on DOMAIN prediction (see Fig. 1 caption for explanation).

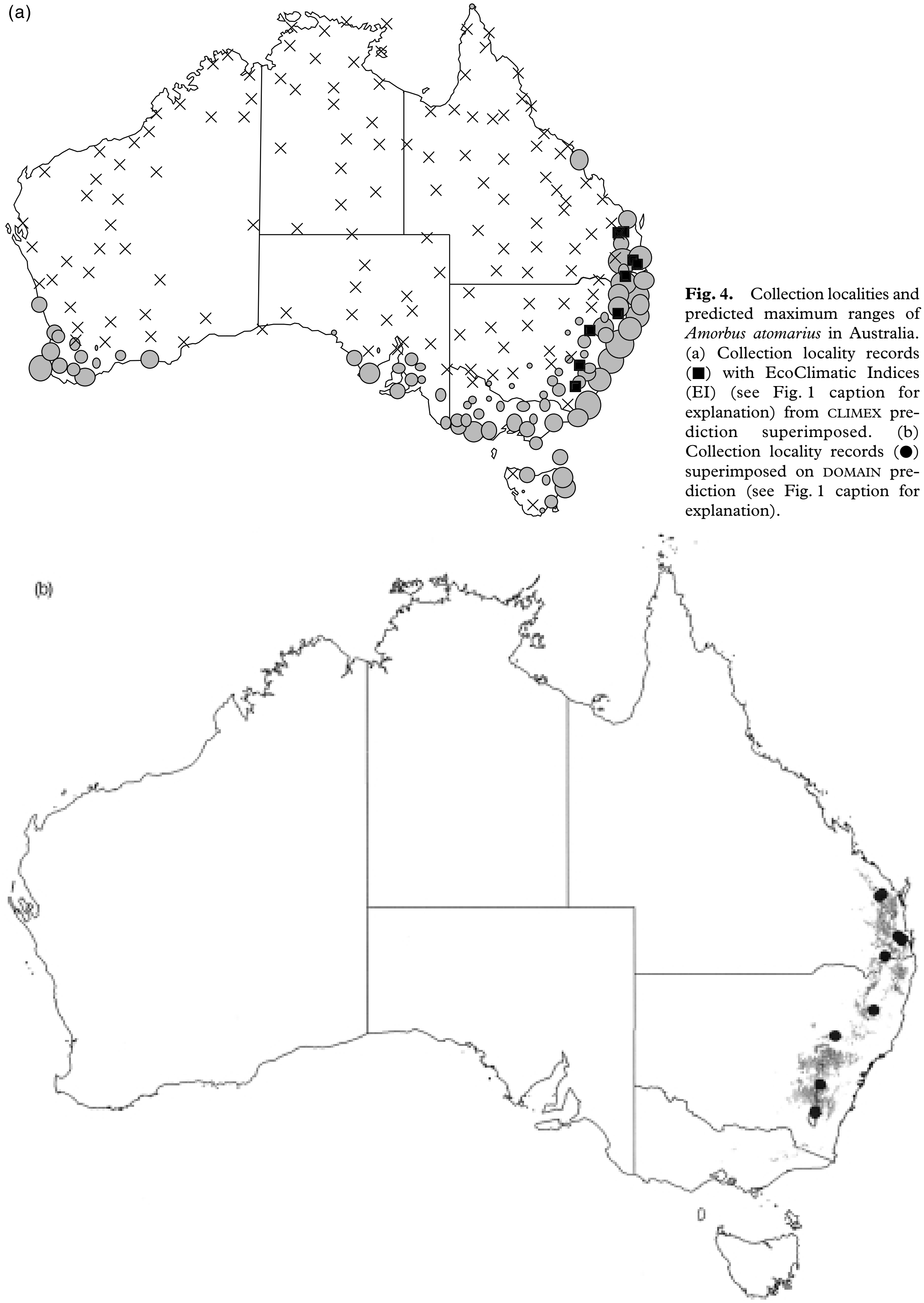


Fig. 4. Collection localities and predicted maximum ranges of *Amorbus atomarius* in Australia. (a) Collection locality records (■) with EcoClimatic Indices (EI) (see Fig. 1 caption for explanation) from CLIMEX prediction superimposed. (b) Collection locality records (●) superimposed on DOMAIN prediction (see Fig. 1 caption for explanation).

disjunct regions, southern, central and northern Australia (Fig. 3b). The temperature range obtained for this species using BIOCLIM is the widest of any of the species considered (Table 3). Given that the collection records for this species comprise coastal as well as inland areas, a wide temperature range might be expected.

Amorbus atomarius

The only host plant record available for this insect is that of a '*Eucalyptus* sp.' which adds little to interpreting the apparently narrow region of endemism (12 unique collection records; Fig. 4a,b, Table 1). The collection records suggest that this species is restricted to the more mountainous regions of the Australian Capital Territory, New South Wales and southern Queensland. If systematic searching for this species confirms that it is in fact restricted to the region shown, high host plant specificity could be a causal mechanism (see comments concerning *Am. bispinus*). For example, there are only two species of eucalypt (*E. dealbata* and *E. eugenioides*) that have distributions closely resembling that of *Am. atomarius*. Using CLIMEX, we were not able to match closely the collection records (Fig. 4a). The maximum geographical range predicted using DOMAIN matched more closely the collection records for this insect (Fig. 4b). The bioclimatic parameters obtained for this species using BIOCLIM are typical of temperate regions on the Australian mainland (Table 3).

Amorbus biguttatus

Eight unique collection records are recorded for *Am. biguttatus* (Fig. 5a,b). While the distribution of *E. miniata* would appear to match closely the northern part of the distribution of *Am. biguttatus*, the same does not apply for *E. camaldulensis*. *Eucalyptus camaldulensis* is eurytopic, whereas *Am. biguttatus* is apparently not. If the collection records are a good approximation of the geographical range of this insect, then the species must have a narrower climatic tolerance than *E. camaldulensis*. The collection records suggest a wet to wet–dry tropics distribution for *Am. biguttatus*, which can be supported by the CLIMEX prediction (Fig. 5a, Table 2). Again, the DOMAIN predicted distribution is considerably more restricted than the CLIMEX prediction (Fig. 5b). The MAT estimated for *Am. biguttatus* with BIOCLIM is the largest of any of the species considered (Table 3). Given that the collection records for this species comprise regions of northern Australia, this result is as expected. Those near coastal collection records in tropical regions are also characterized by a narrow temperature range and high annual rainfall, as estimated using BIOCLIM (Table 3).

Amorbus bispinus

This species is restricted to south-west Western Australia and has presently only been recorded from Jarrah, *E. marginata* (18 unique collection records; Fig. 6a,b). The distributions of *E. marginata* and *Am. bispinus* show a very high degree of overlap. However, the Geraldton (114°37′E, 28°46′S) collection locality to the north of Perth does not coincide with the known distribution of *E. marginata*, possibly suggesting that this insect may be able to feed on some other eucalypt species. In order to model the possible bioclimatic profile of this species, we modified the Mediterranean CLIMEX template (Fig. 6a; Table 2). However,

Table 4. Bioclimatic data from BIOCLIM predictions based on collection records of *G. tasmanicus* and *Am. obscuricornis* in Tasmania

Elevation interval (a.s.l.; in m)	MAT	minTCM	maxTHM	Range	MTCQ	MTWQ	MTHQ	MTDQ	AR
1–50 (20)	12.6	4.8	21.8	16.9	9.0	9.8	16.3	15.7	999
51–100 (71)	12.1	4.1	21.8	17.6	8.4	9.6	16.0	15.2	1101
101–150 (129)	11.6	3.5	21.7	18.1	7.8	8.5	15.6	15.2	1357
151–200 (173)	11.2	2.6	22.0	19.4	7.1	8.1	15.4	15.2	1218
201–250 (224)	10.8	2.8	21.4	18.6	6.9	7.6	14.9	14.8	1588
251–300 (271)	10.6	2.4	21.5	19.0	6.6	8.1	14.8	14.7	1349
301–350 (326)	10.2	2.2	20.9	18.6	6.3	7.5	14.3	14.3	1580
351–450 (396)	9.8	2.0	20.5	18.4	5.9	7.2	14.0	14.0	1645
451–650 (544)	8.9	1.5	19.4	17.9	5.1	5.9	13.1	13.1	1749
651–850 (753)	7.7	0.4	18.2	17.8	3.8	4.4	12.0	12.0	1784
851–1050 (948)	6.5	–0.8	17.1	17.9	2.4	2.7	11.0	11.0	1725
1051–1250 (1134)	5.4	–2.0	16.0	17.9	1.2	1.2	10.1	10.1	1563
Overall (309)	10.5	2.7	20.7	18.0	6.6	7.6	14.6	14.3	1408

Key to bioclimatic index abbreviations given in Appendix I. $n = 88$ individual grid references for *G. tasmanicus*; $n = 103$ individual grid references for *Am. obscuricornis*; 24% of species' grid references are identical. Mean elevation within each interval given in parentheses; highest elevation calculated for which there is a collection record = 1230 m.

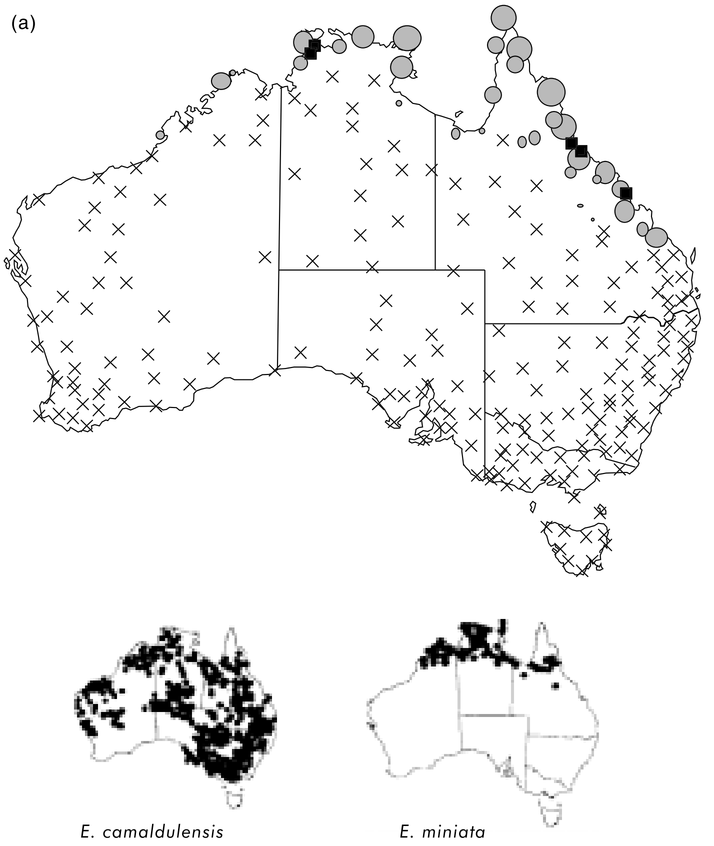
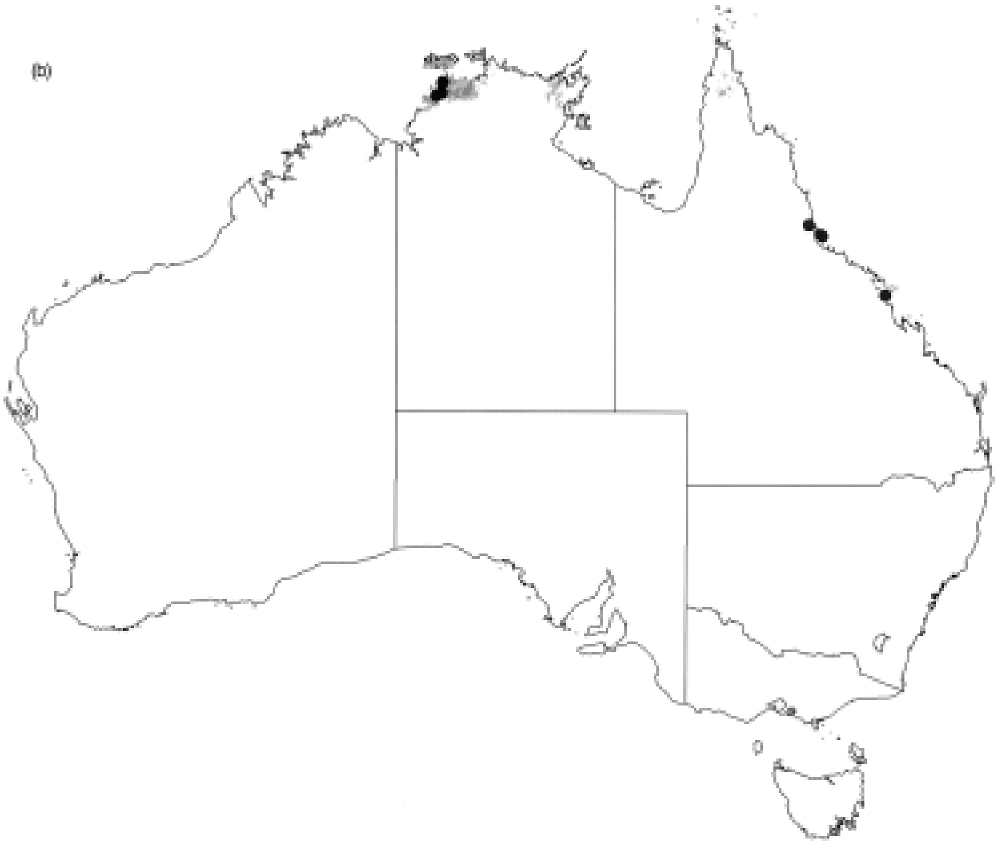


Fig. 5. Collection localities and predicted maximum ranges of *Amorbus biguttatus* in Australia. (a) Collection locality records (■) with EcoClimatic Indices (EI) (see Fig. 1 caption for explanation) from CLIMEX prediction superimposed. Ranges of eucalypt hosts, reproduced from Chippendale (1988), shown below map. (b) Collection locality records (●) superimposed on DOMAIN prediction (see Fig. 1 caption for explanation).



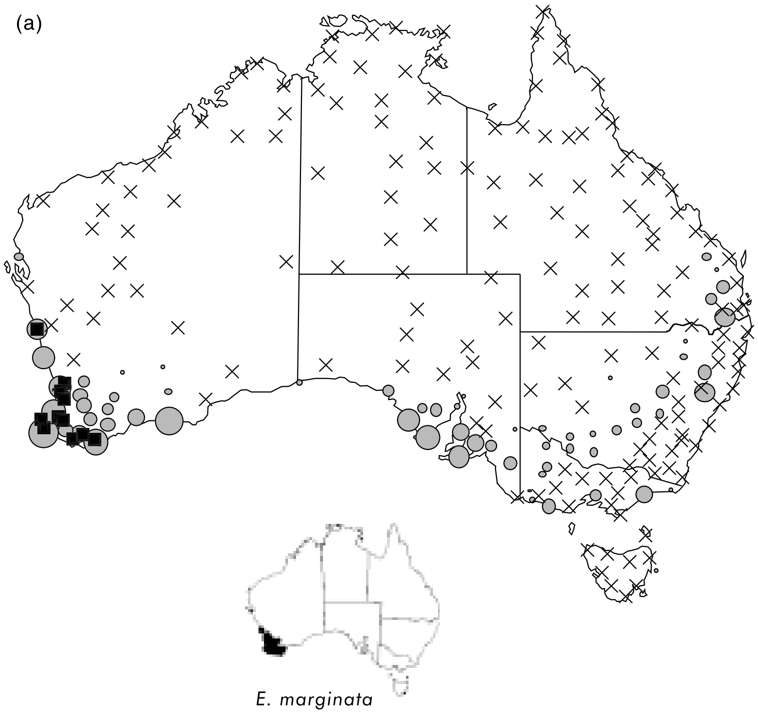


Fig. 6. Collection localities and predicted maximum ranges of *Amorbus bispinus* in Australia. (a) Collection locality records (■) with EcoClimatic Indices (EI) (see Fig. 1 caption for explanation) from CLIMEX prediction superimposed. Range of a eucalypt host, reproduced from Chippendale (1988), shown below map. (b) Collection locality records (●) superimposed on DOMAIN prediction (see Fig. 1 caption for explanation).

Mediterranean-type climates are not only restricted to the south-west corner of Western Australia, so the CLIMEX predicted distribution for *Am. bispinus* encompasses a wider area than the collection records. This could suggest that host plant specificity is the main factor determining this insect's region of endemism. We obtained a very close match to the observed distribution of *Am. bispinus* using DOMAIN (Fig. 6b). The bioclimatic parameters obtained using BIOCLIM resemble those of the species' geographical distribution (Table 3).

Amorbus obscuricornis

This species has a distribution that apparently encompasses most of south-east Australia (extending into southern Queensland) and a number of plant species (106 unique collection records; Fig. 7a,b, Table 1). There is also one record of occurrence in Adelaide from cultivated *E. globulus* (this eucalypt is not endemic to South Australia). Regional 'bridging' of South Australia and southern Victoria could be explained by the occurrence of hosts such as *E. ovata* and *E. viminalis*. Such an explanation seems the most plausible, as this

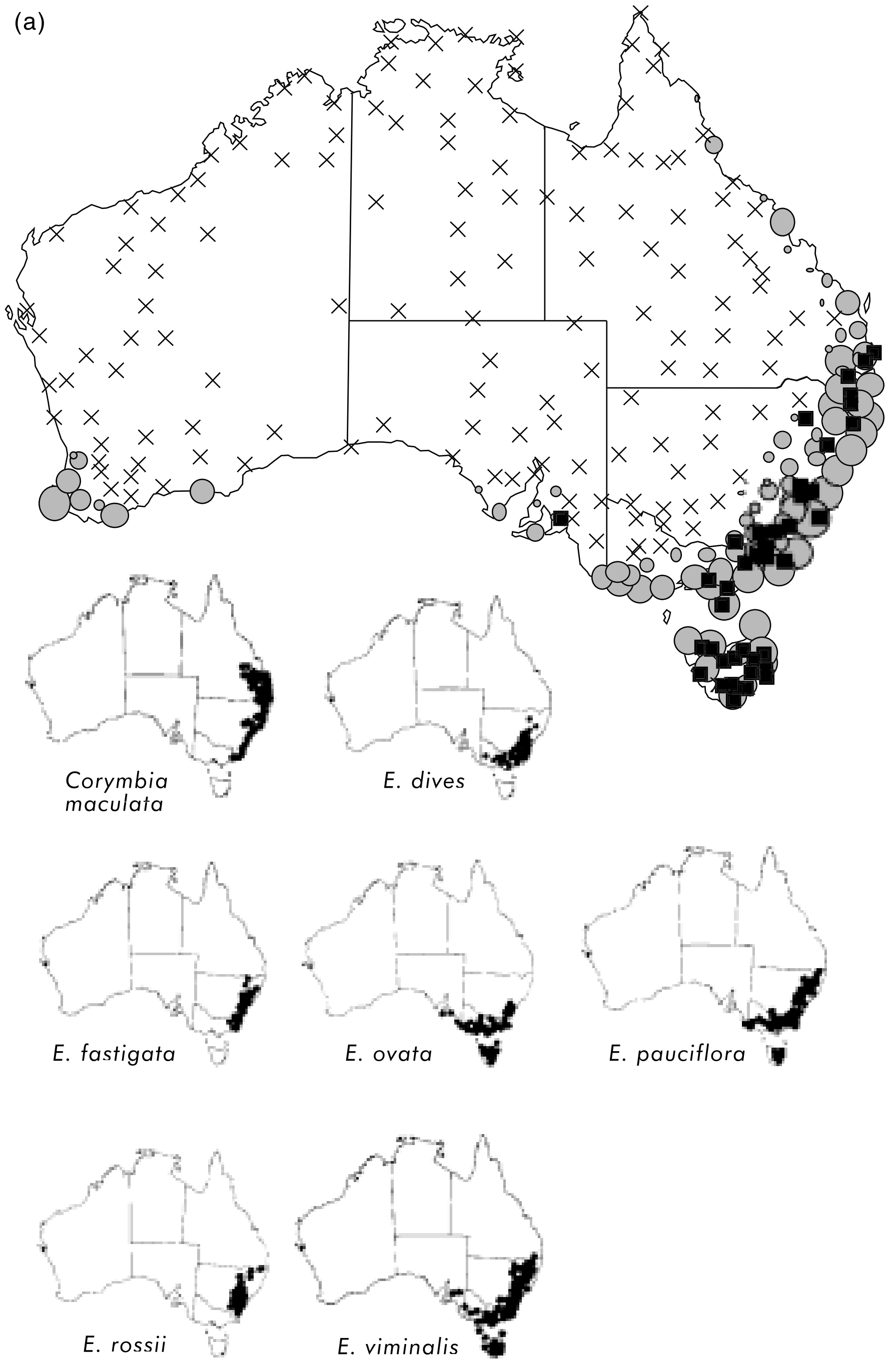


Fig. 7. Collection localities and predicted maximum ranges of *Amorbus obscuricornis* in Australia. (a) Collection locality records (■) with EcoClimatic Indices (EI) (see Fig. 1 caption for explanation) from CLIMEX prediction superimposed. Ranges of selected hosts, reproduced from Chippendale (1988), shown below map (complete list given in Table 1). (b) Collection locality records (●) superimposed on DOMAIN prediction (see Fig. 1 caption for explanation).

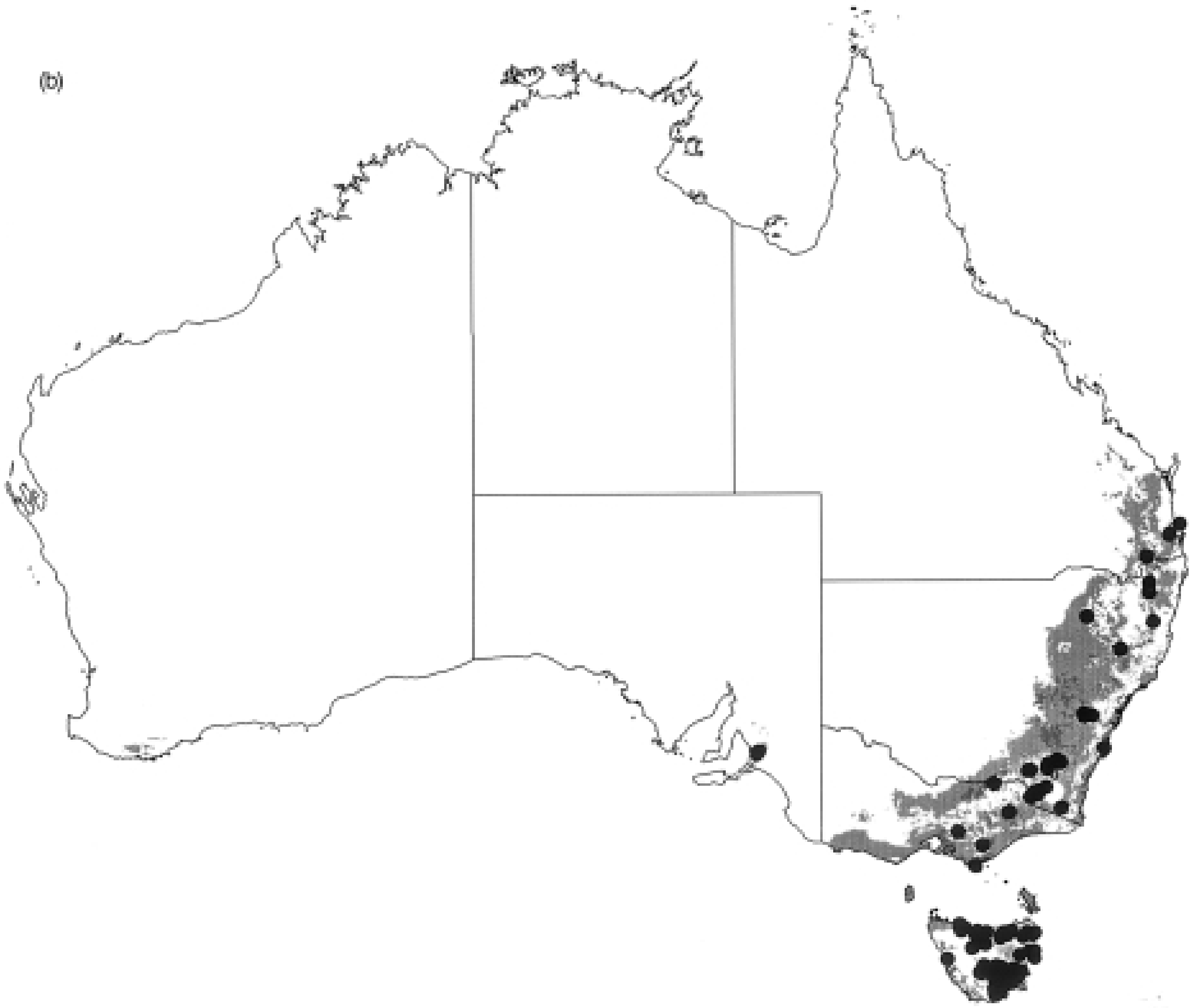


Fig. 7. continued

species does not appear to be a frequent and/or strong flier (M. J. Steinbauer, pers. obs.). The CLIMEX parameter file for this species (Table 2) uses a value for DV0 given by Steinbauer (1997a). Steinbauer (1997a) calculated that 509 degree-days (DD) above 12°C were needed for eclosion at constant temperatures. However, this estimate proved to be too high a value for PDD, and excluded the species from locations where it was known to occur. The final value of 400 for PDD (Table 2) approximates closely the value of 423 DD, which is equivalent to 147 DD for egg eclosion (Steinbauer 1997a) plus 276 DD for nymphal eclosion under fluctuating temperatures (Steinbauer & Clarke 1998). Although the CLIMEX predicted distribution for *Am. obscuricornis* is similar to that for *G. tasmanicus*, the higher DV0 value of 12°C and the PDD value of 400 result in the south-west portion of Tasmania (i.e. the 'WSW' biogeographic region delimited in Thackway & Cresswell 1995) seeming less suitable for this species than it may be for *G. tasmanicus*. This inference is supported by a single collection record for *Am. obscuricornis* from the western half of Tasmania compared with three or four for *G. tasmanicus*. The DOMAIN prediction is very similar to the CLIMEX prediction, and also indicates that a small region in south-west Western Australia could be climatically suitable for this species (Fig. 7b). The Australia-wide bioclimatic parameters obtained for this species using BIOCLIM are typical of temperate regions and resemble closely those obtained for *G. tasmanicus* (Table 3). Of the two species, and based on the BIOCLIM results, *Am. obscuricornis* would appear to prefer slightly warmer and drier habitats than *G. tasmanicus* (suggested by Steinbauer 1995).

Amorbus rhombifer

The host plant records for this insect closely correlate with the distribution of *Am. rhombifer* in the coastal regions of southern Queensland and New South

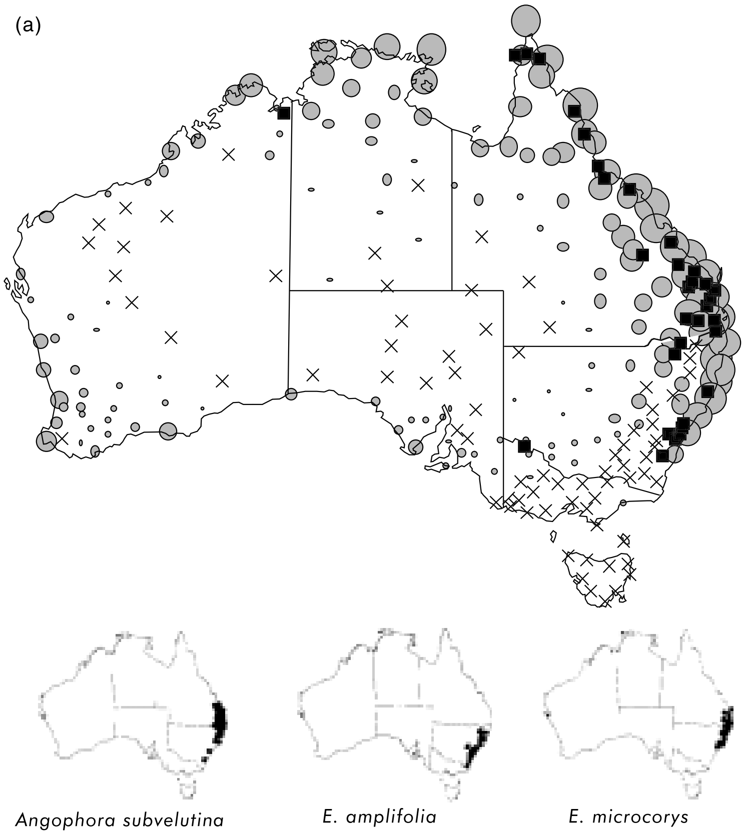
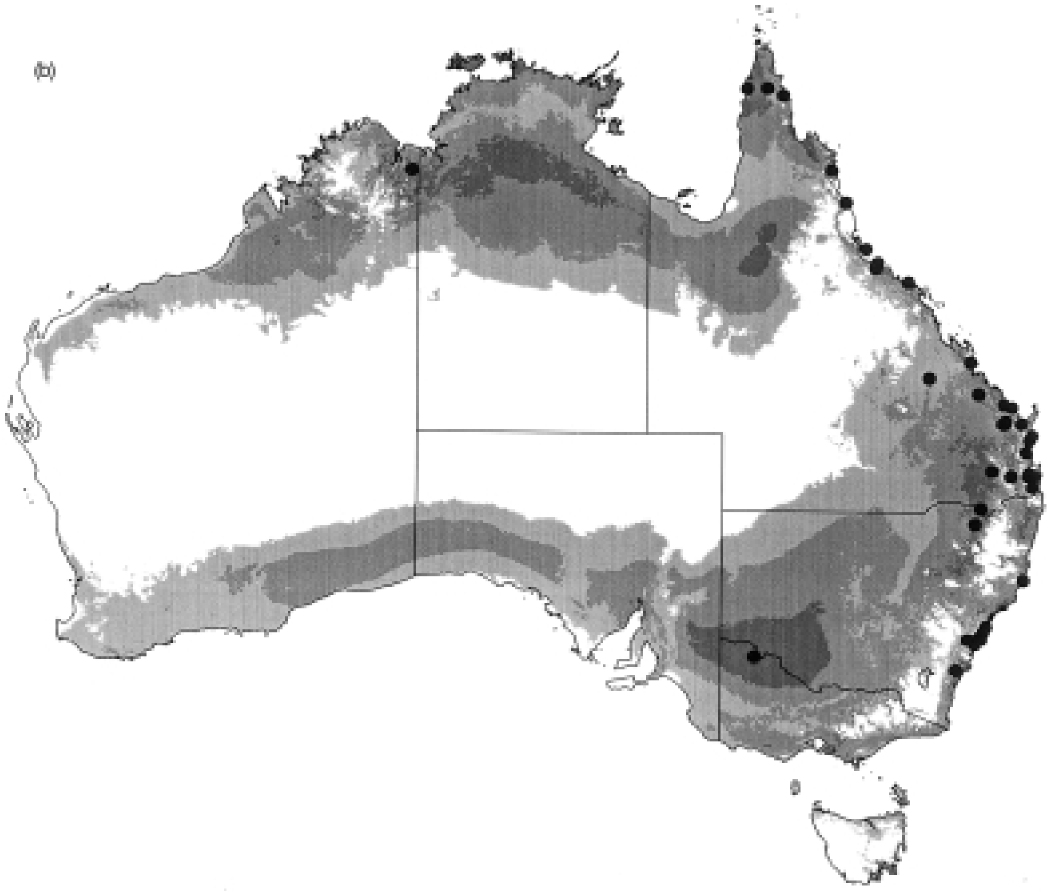


Fig. 8. Collection localities and predicted maximum ranges of *Amorbus rhombifer* in Australia. (a) Collection locality records (■) with EcoClimatic Indices (EI) (see Fig. 1 caption for explanation) from CLIMEX prediction superimposed. Ranges of hosts, reproduced from Chippendale (1988), shown below map. (b) Collection locality records (●) superimposed on DOMAIN prediction (see Fig. 1 caption for explanation).



Wales but not elsewhere (42 unique collection records; Fig. 8a,b). *Amorbus rhombifer* also occurs in Papua New Guinea, where the eucalypt species include *E. alba*, *E. deglupta*, *E. orophila*, *E. urophylla* and *E. wetarensis* (Wood 1959; Ladiges 1997). Of these, only *E. alba* also occurs in Australia. Thus, it seems possible that *E. alba* could also be a host eucalypt of *Am. rhombifer*, although it has not yet been recorded as such. *Eucalyptus alba* is widespread in the Kimberley, Western Australia, across the northern portion of the Northern Territory and in Queensland from Cape York to Rockhampton including coastal islands (Chippendale 1988). The distribution of this eucalypt, together with the other hosts cited in Table 1, matches the entire distribution of *Am. rhombifer*. Using CLIMEX (Fig. 8a; Table 2) it was possible to obtain a potential distribution similar to that of the collection records, with the exception of the south-east portion of Western Australia where this species has not been recorded. The DOMAIN predicted range (Fig. 8b) appears divided into southern and northern halves, linked in Queensland by a thin coastal region of high climatic similarity. The differences between the CLIMEX and DOMAIN predictions will only be resolved after a re-examination of the species' identifications and additional collecting, in particular from Papua New Guinea, Melville Island, and regions around Katherine, Townsville and Mildura. The bioclimatic parameters estimated for *Am. rhombifer* using BIOCLIM are typical of warm, moist habitats; however, the temperatures presented in Table 3 are considerably lower than DV2 and DV3 used in the CLIMEX model.

Amorbus robustus

Fifty-four unique collection records were available for *Am. robustus* (Fig. 9a,b). The occurrence of *Am. robustus* in the arid regions of central Australia may be associated with the distribution of one of its hosts, *E. microtheca*. *Amorbus robustus* also occurs in Papua New Guinea and therefore the remarks made concerning eucalypt host plants of *Am. rhombifer* are relevant to this species (see previously). The CLIMEX prediction suggests that most of the continent could be suitable for this species, with the possible exception of the high altitude regions of the south-east mainland as well as Tasmania (Fig. 9a). The DOMAIN prediction (Fig. 9b) largely concurs with the CLIMEX prediction. However, the DOMAIN prediction indicates a higher suitability for the semiarid and arid regions where some collections were made. The bioclimatic parameters estimated using BIOCLIM for this species cover the spectrum of temperatures typical of the climate across much of mainland Australia, as might be expected for an apparently ubiquitous species (Table 3).

Amorbus rubiginosus

Of all the *Amorbus* species, *Am. rubiginosus* is the most widely distributed (126 unique collection records; Fig. 10a,b). It has been recorded from all states and territories with the exception of Tasmania. None of the recorded hosts of *A. rubiginosus* (Table 1) occur in Tasmania. Collection records from Victoria and New South Wales come from high altitude and non-coastal localities, whereas in Queensland they are predominantly confined to coastal regions. Only in Western Australia and the Northern Territory does there appear to be any significant extension of the species into more arid inland regions. Not surprisingly, the distributions of the species' known eucalypt hosts correlate well with the distribution of *Am. rubiginosus*. The CLIMEX prediction (Fig. 10a; Table 2) indicates that most regions of Australia should be suitable for this species, the only exclusions being some desert regions in northern Western Australia, Thredbo (1380 m a.s.l.) in alpine New South Wales and a couple of regions on the west coast of Tasmania. The prediction obtained using DOMAIN (Fig. 10b) broadly resembles that obtained using CLIMEX. The bioclimatic parameters for *Am. rubiginosus* derived using BIOCLIM are generally mesic in comparison with those of other species considered herein (Table 3).

Climatic profile of *G. tasmanicus* and *Am. obscuricornis* habitats in Tasmania

The BIOCLIM results are summarized according to elevation above sea level (Table 4). Habitats at elevations up to 100 m a.s.l. are best suited to the development of eggs and nymphs of *Am. obscuricornis* (Table 4). These habitats have an MAT of 12.1°C, which is close to the developmental threshold temperatures of 11.8 and 12.0°C estimated for egg and nymphal eclosion, respectively, for *Am. obscuricornis* (Steinbauer 1997a). In contrast, habitats up to 250 m a.s.l. appear suitable for the development of *G. tasmanicus*. These sites have a MAT identical to the developmental threshold temperature for egg eclosion, 10.8°C (Steinbauer 1997a). Based on MTWQ, *Am. obscuricornis* would survive best in refuges at elevations less than 50 m a.s.l., whereas *G. tasmanicus* could survive in refuges at elevations up to approximately 850 m a.s.l. (Steinbauer 1998). The MTWQ, rather than MTCQ, is considered the most relevant parameter to consider with respect to overwintering requirements, because prolonged starvation-longevity requires high relative humidities (Steinbauer 1998). Both the CLIMEX parameters (Figs 1,7; Table 2) and the BIOCLIM (Table 4) results support suggestions that *G. tasmanicus* is better suited to cooler climates than *Am. obscuricornis* (suggested in Steinbauer 1997a, 1997b, 1998).

DISCUSSION

For whatever reasons, coreids are quite often rare or, at best, locally abundant species (see Figs 1c,d, 2c,d in Steinbauer 1997b). As a consequence, the study of their biology, let alone their ecology, is always likely to be fraught with difficulty. In the case of such organisms, abundant specimens for study can only be obtained over long periods of time. It is for this reason that reference collections are so valuable. No enthusiast could possibly hope to collate such a collection even during a lifetime of survey expeditions. In the present study we have used the combined 'observations' of many entomologists over a long period of time to infer the same amount of information, if not more, about the biology and ecology of eight previously unstudied coreid species than the senior author gleaned about two species in 3.5 years of dedicated study. Clearly, the value of such reference collections cannot be overstated.

Using the specimen labels of these coreids, we obtained maps of known collection localities, some data on possible host plants as well as the insects' seasonal

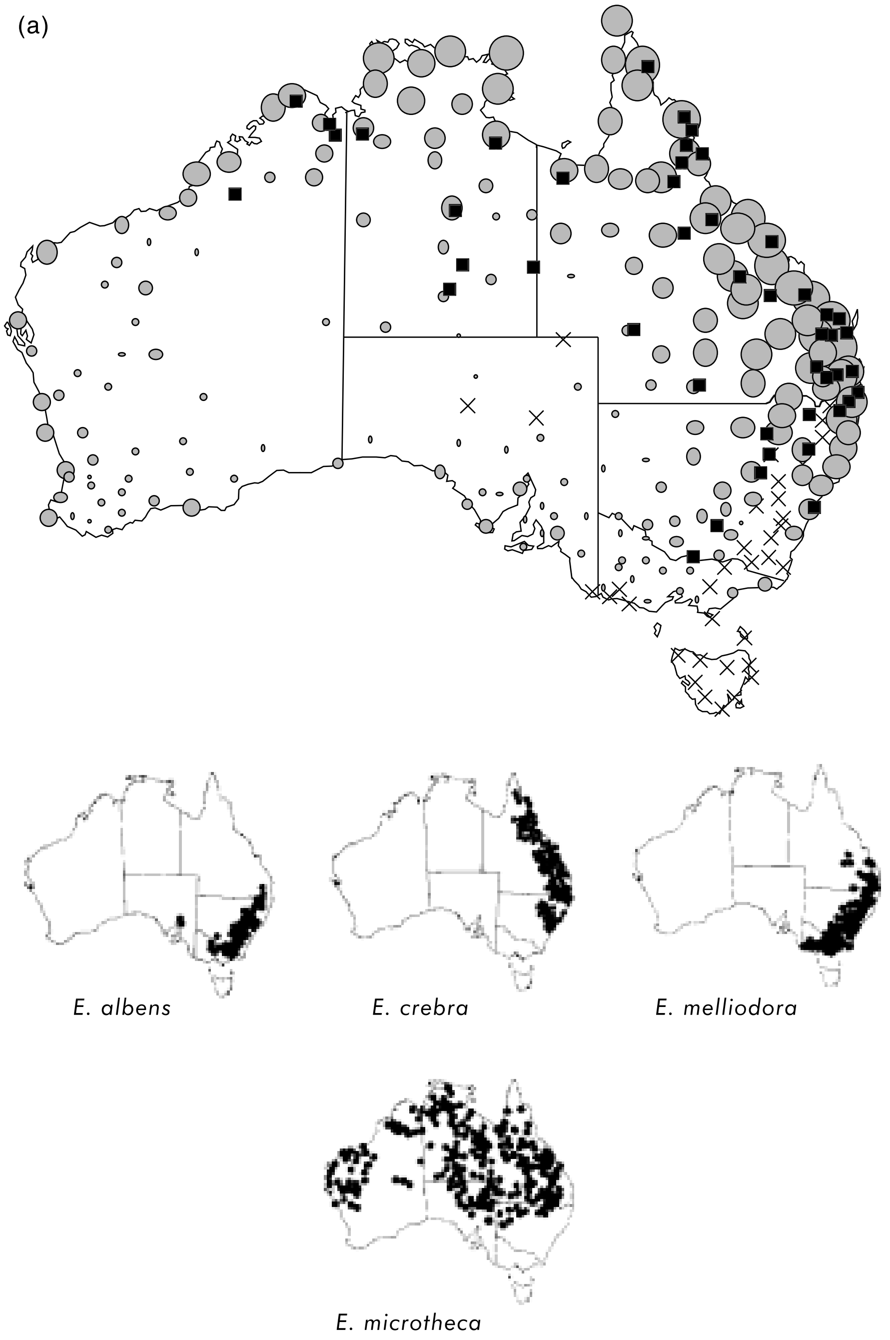


Fig. 9. Collection localities and predicted maximum ranges of *Amorbus robustus* in Australia. (a) Collection locality records (■) with EcoClimatic Indices (EI) (see Fig. 1 caption for explanation) from CLIMEX prediction superimposed. Ranges of eucalypt hosts, reproduced from Chippendale (1988), shown below map. (b) Collection locality records (●) superimposed on DOMAIN prediction (see Fig. 1 caption for explanation).

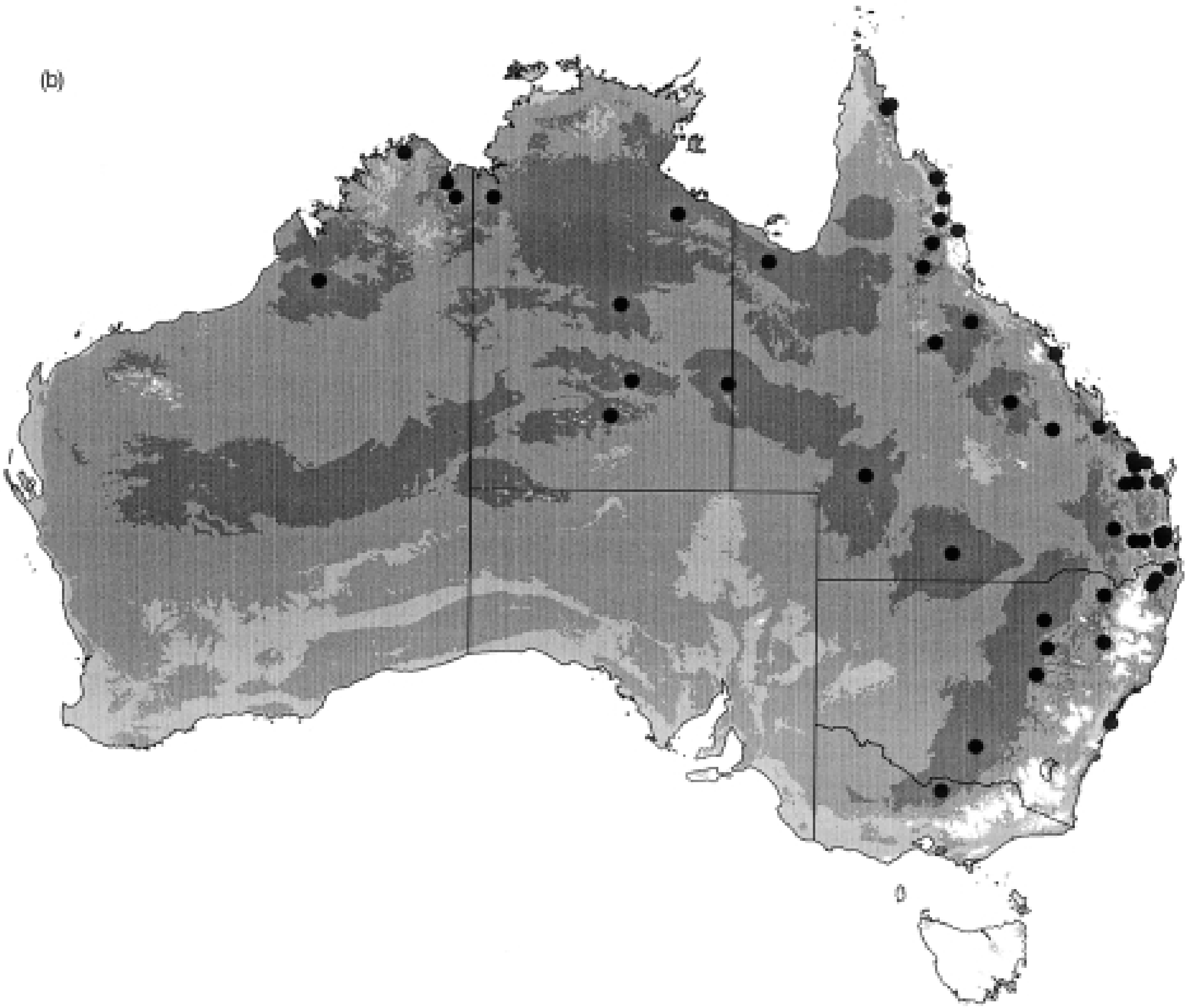


Fig. 9. continued

phenologies. Based on some of these data we then obtained predicted maximum geographical ranges and the environmental characteristics of collection localities. We point to the similarity between the experimentally derived biological data for *G. tasmanicus* and *Am. obscuricornis* and the bioclimatic values estimated using BIOCLIM, in particular those from Tasmania, as proof of the validity of inferring preliminary insights about a species using such packages. Hence, correlative distribution-modelling programs provide a supplementary tool to infer additional information about an organism or taxon when only limited empirical data exist, for example a few collection locality records. An apparently reasonable follow-on question might then be 'how accurate are process-based distribution-modelling predictions when data derived from correlative distribution-modelling programs are inserted into the species' specific parameter values?' Were such an approach to prove valid, we might infer yet more about an organism's biology in the absence of the opportunity to conduct experimental developmental studies under controlled conditions. Perhaps such predictions could be used as comparisons with predicted distributions obtained through matching predicted and know distributions via reiterative simulations.

CLIMEX has often been used to investigate the likelihood of establishment and spread of introduced insect species (Worner 1988; Hughes & Maywald 1990; Scott 1992; Spradbery & Maywald 1992). Often these predictions are modified based on knowledge of how favourable a particular location or locations are for the species concerned, that is, relative abundance estimates for different regions. The data we used in this work provided for only one record per collection locality and did not provide grid references for regions where the species is not known to occur. As a result, the relative suitability of locations could not be used to improve predictions. Such information should be used in conjunction with empirically derived biological data in future CLIMEX predictions concerning these insects.

Studies of the developmental biology of Australian coreids will provide actual parameter values for use in CLIMEX models; however, soil moisture requirements of the host eucalypts could improve such predictions even further. Steinbauer (1999) suggested that seasonal variation in eucalypt shoot production, as influenced by temperature and the availability of soil moisture, was important to the ecology of *Amorbus* species. Scott and Yeoh (1999) employed previously published information about the moisture requirements of the host plant *Emex australis* in their model of the predicted distribution of the aphid *Brachycaudus rumexicolens* in Australia. Unfortunately, a similar approach was not possible for the present study. This was because of the

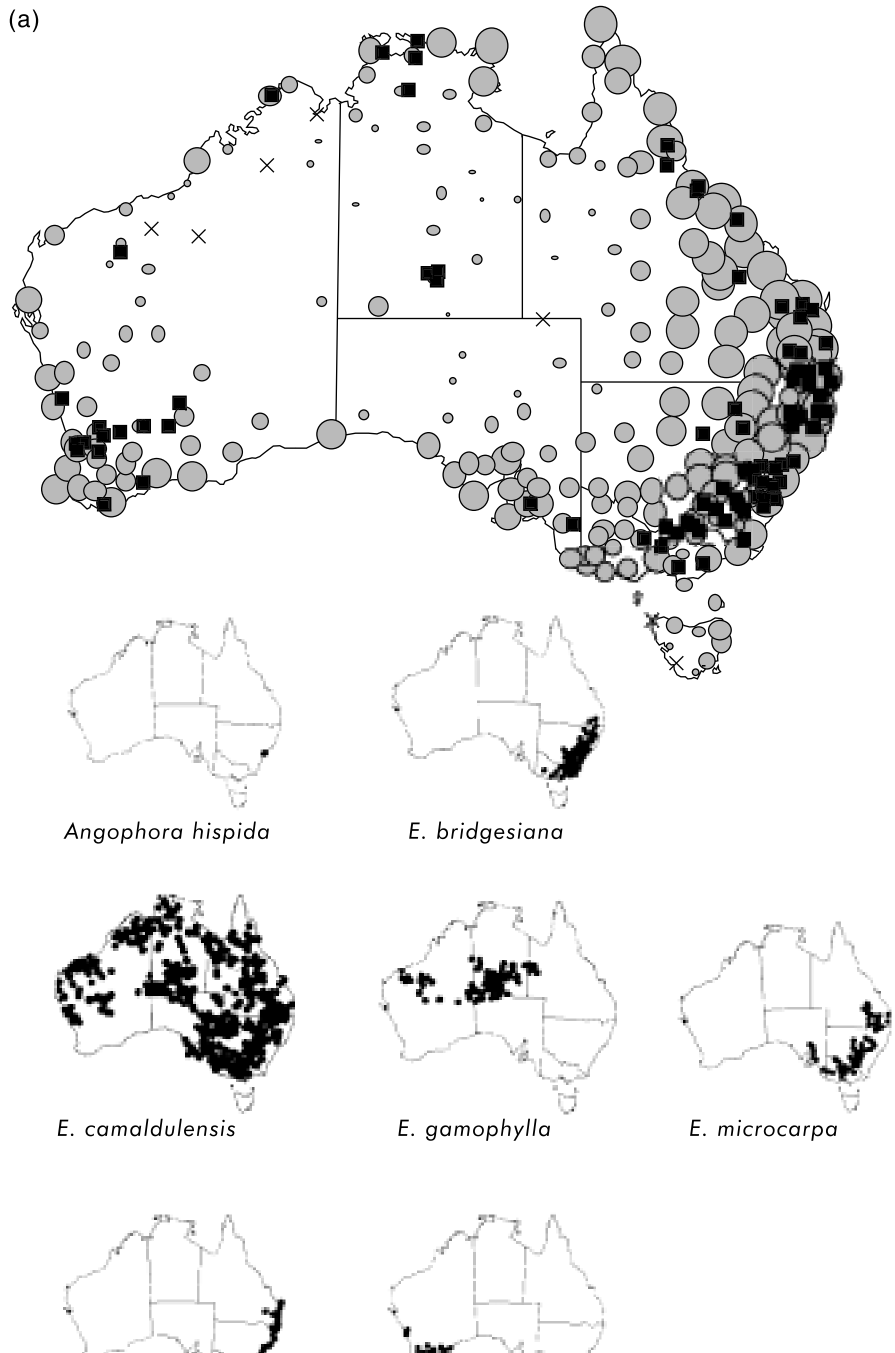


Fig. 10. Collection localities and predicted maximum ranges of *Amorbus rubiginosus* in Australia. (a) Collection locality records (■) with EcoClimatic Indices (EI) (see Fig. 1 caption for explanation) from CLIMEX prediction superimposed. Ranges of selected hosts, reproduced from Chippendale (1988), shown below map (complete list given in Table 1). (b) Collection locality records (●) superimposed on DOMAIN prediction (see Fig. 1 caption for explanation).

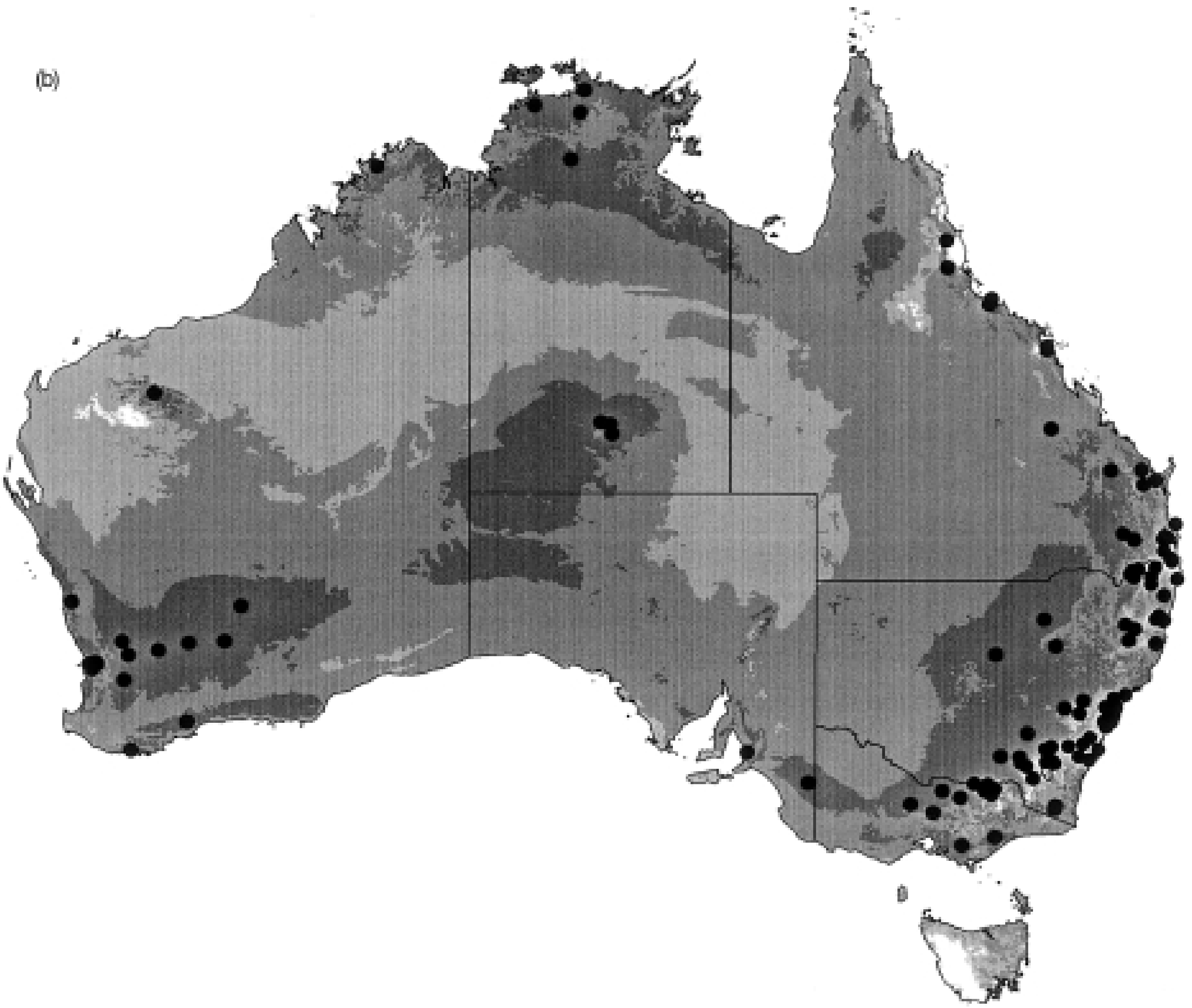


Fig. 10. continued

paucity of host records for some coreids, the great number of eucalypts recorded for other bugs and the lack of detailed information concerning the growth responses of many of these eucalypts to variations in temperature and soil moisture (but see Hughes *et al.* 1996). In addition, without any means of assigning the relative preference of the coreid for certain of these eucalypts, it is difficult to determine which host to focus on.

The present study has shown that *Am. atomarius*, *Am. obscuricornis*, *Am. rhombifer*, *Am. robustus* and *Am. rubiginosus* all occur in southern NSW. These 'near-coastal regions of New South Wales' correspond to the region where Chippendale (1988) suggested that *Eucalyptus* attains its greatest diversity (Chippendale 1988; Wardell-Johnson *et al.* 1997). Carver *et al.* (1991) considered that, of the Coreinae, only the genus *Amorbus* appeared to have undergone any degree of evolutionary radiation in Australia. These findings support the hypothesis that the evolutionary radiation of *Amorbus* may have followed the radiation of the eucalypts (Fig. 11; see Hill 1994). In contrast, only two species of *Amorbus*, namely *Am. bispinus* and *Am. rubiginosus*, have been recorded from the south-west of Western Australia. This region is also noted as an area of high eucalypt diversity (Chippendale 1988). However, the diversity of *Amorbus* seems comparatively low in south-west Western Australia (Fig. 11). Wardell-Johnson *et al.* (1997) noted that 'the mosaic of eucalypt species is at a finer scale in the forests of south-east Australia and Tasmania than in the forests of south-west Australia or the woodlands of northern Australia'. They suggest that the greater topographic complexity in south-east Australia prevents individual eucalypt species from dominating the landscape as occurs in south-west Australia. It is possible that this factor could explain the difference in *Amorbus* species diversity. Furthermore, such a difference might provide an explanation for the apparent restriction in degree of oligophagy exhibited by species such as *Am. bispinus*.

The jarrah forests of south-west Western Australia have been logged and cleared since 1829, with the rate of logging reaching a peak from 1950 to 1975 (Mazanec & Justin 1994). Thus, one might suspect that this activity could have reduced the habitat available to species of *Amorbus*. However, examination of the collection records questions this suggestion. For example, the next oldest specimens of *Am. bispinus* after the syntypes described by Westwood in 1842 date from 1913 and were collected in the Darlington and Geraldton regions, whereas the most recent specimen dates from 1990 and was collected from Denmark. Hence, this species continued to be collected throughout the period of heaviest logging. A similar statement can be made concerning the records of *Am. rubiginosus* for the south-west region of Western Australia. Furthermore, a number of specimens of *Am. bispinus* dating from 1966 and 1972 (from the Kirup and Dwellingup regions, respectively) are recorded as being collected from '*E. marginata* regrowth' and '*E. marginata* suckers'. This suggests that logging was resulting in the production of greater amounts of coppice in the general area and may have actually favoured species such as *Am. bispinus*. Such behaviour accords well with the preference of members of the genus generally for coppice vegetation (see Steinbauer 1999). Where tree clearing has been followed by widespread and intensive urbanization (i.e. the complete removal of tree stumps), some species of *Amorbus* do not appear to have persisted, at least on a local scale. For example, the single female holotype of *Am. robustus*, which was described by Mayr in 1865, represents the only collection record of this species for Sydney.

Only *G. tasmanicus* and *Am. obscuricornis* occur on the Australian mainland as well as in Tasmania. This situation might have arisen if *Am. obscuricornis* and *G. tasmanicus* arrived in Tasmania during the Oligocene–Miocene period before the initial rise in sea level separated the two land masses some 25 million years ago (Barlow 1981; Wilford & Brown 1994). Both species could have survived the climatic changes in the Pleistocene, perhaps with minor alterations in distribution and adapting to a wider range of eucalypt hosts following changes in certain species availability (Burbidge 1960; Barlow 1981). Other mainland *Amorbus* species may have been concomitantly prevented from expansion into pleniglacial Tasmania because of limited forested regions/habitat diversity, cooler climate and/or lack of hosts (Davies 1974; Barlow 1981). With the most recent severance of the

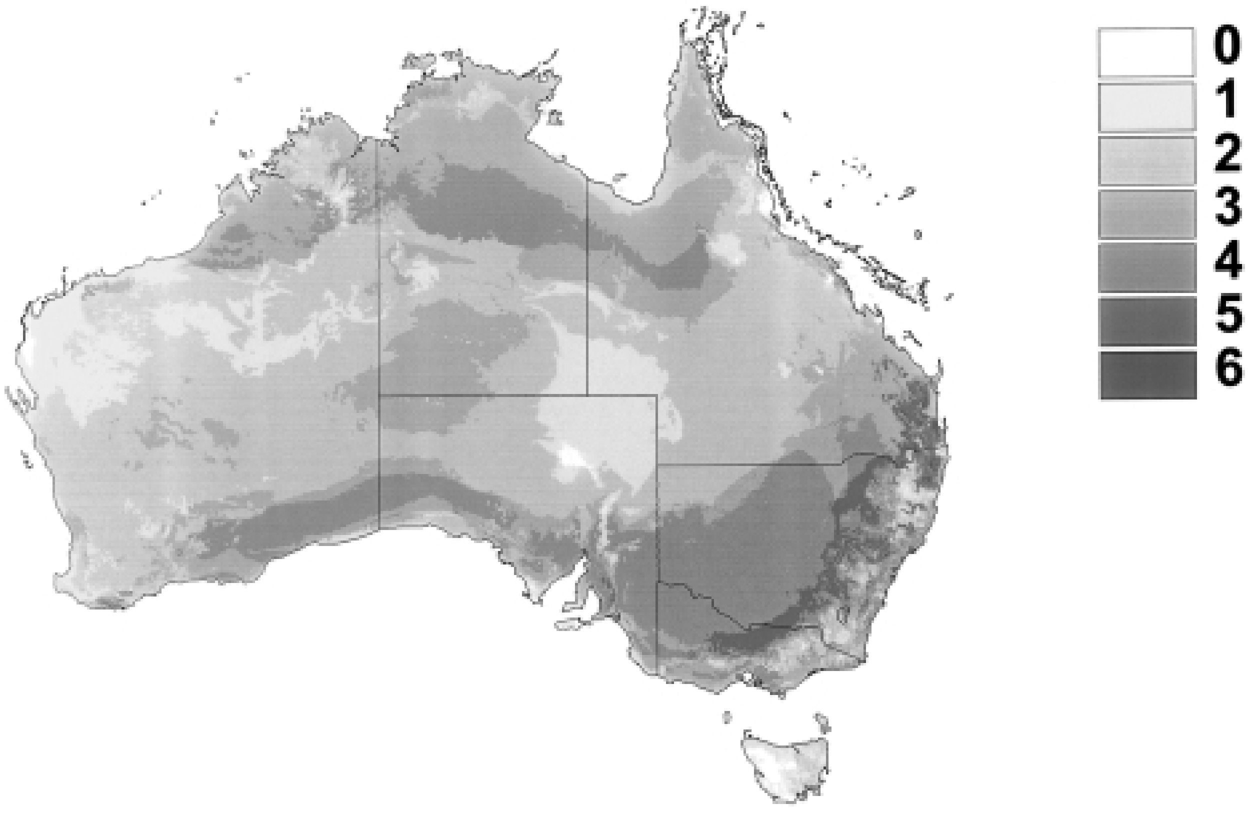


Fig. 11. *Amorbus* species diversity map for Australia (coastal reefs not included in prediction). Key: 0, no species; 6, many species.

land bridge between Australia and Tasmania during the late Pleistocene (some 12–13.5 thousand years ago), what had once been single populations of *Am. obscuricornis* and *G. tasmanicus* were again divided into mainland and Tasmanian populations (Davies 1974). In support of this scenario, Pryor (1976) suggested that the endemic Tasmanian eucalypt species did not arise following the separation of Tasmania from the mainland but may represent relict species that were once more widely distributed. It was suggested that such eucalypts might have evaded competition with other eucalypt species by inhabiting 'special' habitats (Pryor 1976). Such a hypothesis would support the suggestion that the host eucalypts of *Am. rubiginosus* might once have been the invading tree species. Their being prevented from reaching Tasmania also excluded *Am. rubiginosus*.

We hope that the present work might foster interest in the use of institutional collections as sources of information about taxa under investigation. The example provided by our study has posed a number of questions concerning Australian Coreidae that we hope others may attempt to clarify. A number of these questions would not have come to light without using the approaches referred to herein. Thus, we attest to having found the insights provided by both the process and correlative distribution modelling programs thought provoking to say the least.

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REFERENCES

Allsopp P. G. (1995) Biogeography of the Australian Dynastinae, Rutelinae, Scarabaeinae, Melolonthini, Scitalini and Geotrupidae (Coleoptera: Scarabaeoidea). *J. Biogeogr.* **22,** 31–48.

Anonymous (1993) *Climate of Tasmania*. Bureau of Meteorology, Canberra.

Ayres M. P. (1991) Adaptation and constraint in *Papilio canadensis*: Geographic variation in nutritional physiology and temperature responses. PhD Thesis, Michigan State University, Michigan.

Ayres M. P. & Scriber J. M. (1994) Local adaptation to regional climates in *Papilio canadensis* (Lepidoptera: Papilionidae). *Ecol. Monogr.* **64,** 465–82.

Baldwin J. D. & Dingle H. (1986) Geographic variation in the effects of temperature on life-history traits in the large milkweed bug *Oncopeltus fasciatus*. *Oecologia* **69,** 64–71.

Barlow B. A. (1981) The Australian flora: Its origin and evolution. In: *Flora of Australia*. Vol. 1. *Introduction* (ed. A. S. George) pp. 25–75. Australian Government Publishing Service, Canberra.

Burbidge N. T. (1960) The phytogeography of the Australian region. *Aust. J. Bot.* **8,** 75–212.

Carpenter G., Gillison A. N. & Winter J. (1993) DOMAIN: A flexible modelling procedure for mapping potential distributions of plants and animals. *Biodivers. Cons.* **2,** 667–80.

Carver M., Gross G. F. & Woodward T. E. (1991) Hemiptera (Bugs, leafhoppers, cicadas, aphids, scale insects etc.). In: *The Insects of Australia* (ed. CSIRO) pp. 429–509. Melbourne University Press, Carlton.

Chippendale G. M. (1988) *Flora of Australia*. Vol. 19. *Myrtaceae: Eucalyptus, Angophora*. Australian Government Publishing Service, Canberra.

Colless D. H. (1980) Biogeography of Australian Sepsidae (Diptera). *Aust. J. Zool.* **28,** 65–78.

Cranston P. S. & Naumann P. S. (1991) Biogeography. In: *The Insects of Australia* (ed. CSIRO) pp. 180–97. Melbourne University Press, Carlton.

Davidson J. (1934) Climate in relation to insect ecology in Australia. 1. Mean monthly precipitation and atmospheric deficit in Australia. *Trans. Roy. Soc. S. Aust.* **58,** 197–210.

Davidson J. (1935) Climate in relation to insect ecology in Australia. 2. Mean monthly temperature and precipitation–evaporation ratio. *Trans. Roy. Soc. S. Aust.* **59,** 107–24.

Davidson J. (1936) Climate in relation to insect ecology in Australia. 3. Bioclimatic zones in Australia. *Trans. Roy. Soc. S. Aust.* **60,** 88–92.

Davies J. L. (1974) II. Geomorphology and Quaternary environments. In: *Biogeography and Ecology in Tasmania* (ed. W. D. Williams) pp. 17–27. Dr W. Junk, The Hague.

Eberhard W. G. (1998) Sexual behaviour of *Acanthocephala declivis guatemalana* (Hemiptera: Coreidae) and the allometric scaling of their modified hind legs. *Ann. Entomol. Soc. Am.* **91,** 863–71.

Hill R. S. (1994) The history of selected Australian taxa. In: *History of the Australian Vegetation: Cretaceous to Recent* (ed. R. S. Hill) pp. 390–419. Cambridge University Press, Cambridge.

Hughes L., Cawsey E. M. & Westoby M. (1996) Geographic and climatic range sizes of Australian eucalypts and a test of Rapoport's rule. *Global Ecol. Biogeogr.* **5,** 128–42.

Hughes R. D. & Maywald G. F. (1990) Forecasting the favourableness of the Australian environment for the Russian wheat aphid, *Diuraphis noxia* (Homoptera: Aphididae), and its potential impact on Australian wheat yields. *Bull. Entomol. Res.* **80,** 165–75.

Jeffree E. P. & Jeffree C. E. (1994) Temperature and the biogeographical distributions of species. *Funct. Ecol.* **8,** 640–50.

Kukal O., Ayres M. P. & Scriber J. M. (1991) Cold tolerance of the pupae in relation to the distribution of swallowtail butterflies. *Can. J. Zool.* **69,** 3028–37.

Kumar R. (1966) Studies on the biology, immature stages, and relative growth of some Australian bugs of the superfamily Coreoidea (Hemiptera: Heteroptera). *Aust. J. Zool.* **14,** 895–991.

Ladiges P. Y. (1997) Phylogenetic history and classification of eucalypts. In: *Eucalypt Ecology: Individuals to Ecosystems* (eds J. Williams & J. Woinarski) pp. 16–29. Cambridge University Press, Melbourne.

MacLean Jr S. F. (1983) Life cycles and the distribution of psyllids (Homoptera) in arctic and subarctic Alaska. *Oikos* **40,** 445–51.

Maschwitz U., Fiala B. & Dolling W. R. (1987) New trophobiotic symbioses of ants with south east Asian bugs. *J. Nat. Hist.* **21,** 1097–107.

Mazanec Z. & Justin M. J. (1994) Fecundity and oviposition by *Perthida glyphopa* Common (Lepidoptera: Incurvariidae). *J. Aust. Entomol. Soc.* **33,** 223–34.

McClure M. S. (1989) Importance of weather to the distribution and abundance of introduced adelgid and scale insects. *Agric. For. Meteor.* **47,** 291–302.

McQuillan P. B. (1985) A taxonomic revision of the Australian autumn gum moth genus *Mnesampela* Guest (Lepidoptera: Geometridae, Ennominae). *Entomol. Scand.* **16,** 175–202.

McQuillan P. B. & Ek C. J. (1996) A biogeographical analysis of the Tasmanian endemic Ptunarra brown butterfly, *Oreixenica ptunarra* Couchman (Lepidoptera: Nymphalidae: Satyrinae). *Aust. J. Zool.* **44,** 21–37.

Mitchell P. L. (1980) Combat and territorial defense of *Acanthocephala femorata* (Hemiptera: Coreidae). *Ann. Entomol. Soc. Am.* **73,** 404–8.

Moore K. M. (1972) Observations on some Australian forest insects 26. Some insects attacking three important tree species. *Aust. Zool.* **17,** 30–9.

Nix H. (1986) A biogeographic analysis of Australian elapid snakes. In: *Atlas of Elapid Snakes of Australia* (ed. R. Longmore) pp. 4–15. Australian Government Publishing Service, Canberra.

Pearsall W. H. (1950) *Mountains and Moorlands*. Collins, London.

Podger F. D., Mummery D. C., Palzer C. R. & Brown M. J. (1990) Bioclimatic analysis of the distribution of damage to native plants in Tasmania by *Phytophthora cinnamomi*. *Aust. J. Ecol.* **15,** 281–9.

Pryor L. (1976) *The Biology of Eucalypts*. Edward Arnold, Southampton.

Schuh R. T. & Slater J. A. (1995) *True Bugs of the World (Hemiptera: Heteroptera): Classification and Natural History*. Comstock Publishing Associates, Ithaca.

Scott J. K. (1992) Biology and climatic requirements of *Perapion antiquum* (Coleoptera: Apionidae) in southern Africa: Implications for the biological control of *Emex* spp. in Australia. *Bull. Entomol. Res.* **82,** 399–406.

Scott J. K. & Yeoh P. B. (1999) Bionomics and the predicted distribution of the aphid *Brachycaudus rumexicolens* (Hemiptera: Aphididae). *Bull. Entomol. Res.* **89,** 97–106.

Spradbery J. P. & Maywald G. F. (1992) The distribution of the European or German wasp, *Vespula germanica* (F.) (Hymenoptera: Vespidae), in Australia: Past, present and future. *Aust. J. Zool.* **40,** 495–510.

Steinbauer M. J. (1995) The biogeography and host plant utilisation of eucalypt feeding Coreidae (Hemiptera: Heteroptera). PhD Thesis, University of Tasmania, Tasmania.

Steinbauer M. J. (1997a) Seasonal phenology and developmental biology of *Amorbus obscuricornis* (Westwood) and *Gelonus tasmanicus* (Le Guillou) (Hemiptera: Coreidae). *Aust. J. Zool.* **45,** 49–63.

Steinbauer M. J. (1997b) The incidence and relative abundance of *Amorbus obscuricornis* (Westwood) and *Gelonus tasmanicus* (Le Guillou) (Hemiptera: Coreidae) in southern Tasmania and their performance on selected *Eucalyptus* species. *Aust. J. Zool.* **45,** 631–49.

Steinbauer M. J. (1998) Seasonal fluctuations in body weight, lipid content and the starvation-longevity of *Amorbus obscuricornis* (Westwood) and *Gelonus tasmanicus* (Le Guillou) (Hemiptera: Coreidae). *Aust. J. Entomol.* **37,** 90–6.

Steinbauer M. J. (1999) The population ecology of *Amorbus* Dallas (Hemiptera: Coreidae) species in Australia. *Entomol. Exp. Appl.* **91,** 175–82.

Steinbauer M. J. & Clarke A. R. (1996) Revision of the genus *Acantholybas* Breddin (Hemiptera: Coreidae). *Ann. Entomol. Soc. Am.* **89,** 519–25.

Steinbauer M. J. & Clarke A. R. (1998) Field observations of dispersion, mating and development of *Amorbus obscuricornis* (Westwood) (Hemiptera: Coreidae). *Aust. J. Entomol.* **37,** 155–7.

Steinbauer M. J., Clarke A. R. & Paterson S. C. (1998) Changes in eucalypt architecture and the foraging behaviour and development of *Amorbus obscuricornis* (Hemiptera: Coreidae). *Bull. Entomol. Res.* **88,** 641–51.

Stone C., Simpson J. A. & Eldridge R. H. (1998) Insect and fungal damage to young eucalypt trial plantings in northern New South Wales. *Aust. For.* **61,** 7–20.

Sutherst R. W. & Maywald G. F. (1985) A computerised system for matching climates in ecology. *Agric. Ecosyst. Environ.* **13,** 281–99.

Sutherst R. W., Maywald G. F. & Skarratt D. B. (1995) Predicting insect distributions in a changed climate. In: *Insects in a Changing Environment* (eds R. Harrington & N. E. Stork) pp. 59–91. Academic Press, London.

Sutherst R. W., Maywald G. F., Yonow T. & Stevens P. M. (1998) *CLIMEX for Windows*, Version 1.1. User's Guide. Computer software for predicting the effects of climate on plants and animals. CRC for Tropical Pest Management, Brisbane.

Thackway R. & Cresswell I. D., eds (1995) An interim biogeographic regionalisation for Australia. *A Framework for Establishing the National System of Reserves*, Version 4.0. Australian Nature Conservation Agency, Canberra.

Wardell-Johnson G. W., Williams J. E., Hill K. D. & Cumming R. (1997) Evolutionary biogeography and contemporary distribution of eucalypts. In: *Eucalypt Ecology: Individuals to Ecosystems* (eds J. Williams & J. Woinarski) pp. 92–128. Cambridge University Press, Melbourne.

Wilford G. E. & Brown P. J. (1994) Maps of late Mesozoic-Cenozoic Gondwana break-up: Some palaeogeographical implications. In: *History of the Australian Vegetation: Cretaceous to Recent* (ed. R. S. Hill) pp. 5–13. Cambridge University Press, Cambridge.

Williams J. E. (1991) Biogeographic patterns of three subalpine eucalypts in south-east Australia with special reference to *Eucalyptus pauciflora* Sieb. ex Spreng. *J. Biogeog.* **18,** 223–30.

Wood J. G. (1959) The phytogeography of Australia (in relation to radiation of *Eucalyptus*, *Acacia*, etc.). In: *Biogeography and Ecology in Australia* (eds A. Keast, R. L. Crocker & C. S. Christian) pp. 291–302. Uitgeverij Dr W. Junk, Den Haag.

Worner S. P. (1988) Ecoclimatic assessment of potential establishment of exotic pests. *J. Econ. Entomol.* **81,** 973–83.

Yonow T. & Sutherst R. W. (1998) The geographical distribution of the Queensland fruitfly, *Bactrocera (Dacus) tryoni*, in relation to climate. *Aust. J. Agric. Res.* **49,** 935–53.

Zalucki M. P., Murray D. A. H., Gregg P. C., Fitt G. P., Twine P. H. & Jones C. (1994) Ecology of *Helicoverpa armigera* (Hübner) and *H. punctigera* (Wallengren) in the inland of Australia: Larval sampling and host plant relationships during winter and spring. *Aust. J. Zool.* **42,** 329–46.

APPENDIX I

Key to the nine BIOCLIM bioclimatic index abbreviations used herein (temperatures in °C, rainfall in mm)

Abbreviation	Full index name	Abbreviation	Full index name
MAT	Mean annual temperature	MTCQ	Mean temperature of the coolest quarter
minTCM	Mean minimum temperature of the coldest month	MTWQ	Mean temperature of the wettest quarter
		MTHQ	Mean temperature of the hottest quarter
maxTHM	Mean maximum temperature of the hottest month	MTDQ	Mean temperature of the driest quarter
		AR	Annual rainfall
Range	maxTHM – minTCM		

APPENDIX II

Key to the CLIMEX parameter meanings used herein (details concerning the calculation of these parameters are provided in Sutherst & Maywald 1985; Yonow & Sutherst 1998)

Parameter	Parameter meaning	Parameter	Parameter meaning
DV0	Lower temperature threshold	THHS	Heat stress accumulation rate
DV1	Lower optimum temperature	DTHS	Heat stress degree-day threshold (stress accumulates if the weekly number of degree-days above DV3 exceeds this value)
DV2	Upper optimum temperature		
DV3	Upper temperature threshold		
PDD	Number of degree-days above DV0 required to complete a generation		
		DHHS	Heat stress accumulation rate
SM0	Lower soil moisture threshold	SMDS	Soil moisture dry stress threshold
SM1	Lower optimum soil moisture	HDS	Dry stress accumulation rate
SM2	Upper optimum soil moisture	SMWS	Soil moisture wet stress threshold
SM3	Upper soil moisture threshold	HWS	Wet stress accumulation rate
TTCS	Cold stress temperature threshold	TTHW	Hot-wet stress temperature threshold
THCS	Cold stress accumulation rate	MTHW	Hot-wet stress soil moisture threshold
DTCS	Cold stress degree-day threshold (stress accumulates if the weekly number of degree-days above DV0 is below this value)	PHW	Hot-wet stress accumulation rate (defines the rate at which PHW accumulates once the average maximum temperature and the soil moisture exceed TTHW and MTHW, respectively)
DHCS	Cold stress accumulation rate		
TTHS	Heat stress temperature threshold		