



Global climate change and accuracy of prediction of species' geographical ranges: establishment success of introduced ladybirds (Coccinellidae, *Chilocorus* spp.) worldwide

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Abstract

Aim Predictions of how the geographical ranges of species change implicitly assume that range can be determined without invoking climate change. The aim here was to determine how accurate predictions of range change might be before entertaining global climatic change.

Location Worldwide.

Methods All the documented global biological control translocations of ladybirds (Coccinellidae: *Chilocorus* spp.) were analysed with the ecoclimatic program, CLIMEX. This program determines species distributions in relation to climate, and can be used to express the favourableness of different localities for a species. CLIMEX is also a useful exploratory tool for determining the likelihood of establishment of species introduced from one area to another.

Results Predictive models were developed based on the likelihood of establishment of fifteen *Chilocorus* spp. relative to their physiological characteristics and climatic tolerances. This likelihood was compared with actual establishment with a resultant range of 0% accuracy to 100% accuracy. Only four (26.7%) species climatic tolerances could be predicted with 100% certainty. The general lack of accurate prediction was because climate is not always the overriding feature determining whether a species will establish or not. Other determinants, such as localized response to microclimate, phenology, host type and availability, presence of natural enemies and hibernation sites play a varying role over and above climate in determining whether a species will establish at a new locality.

Main conclusions This study shows that even in the absence of climate change, range cannot always be determined, which means that most predictions of range change with climate change are likely to be wrong.

Keywords

Climate change, species geographical range, CLIMEX, prediction, biocontrol

INTRODUCTION

Considerable attention is being given to how species might expand or change their geographical range with global climate change (Peters & Darling, 1985; Cammell & Knight, 1992; Peters, 1991; Brereton *et al.*, 1995). Yet, predictions of geographical range change with global climatic change have two variables. The first is an untested, implicit assumption that we can accurately predict any species range prior to climate change. The second is the one normally considered, and that we can predict changes according to changes in physical climatic

variables. We illustrate here that the first variable cannot be assumed.

One of the tenets of biological control is that natural enemies will be introduced to areas with a similar climate (Franz, 1964; Greathead, 1971). Such introductions are an unplanned, ongoing world experiment that investigates the potential importance of climate matching between a species' area-of-origin and area-of-introduction (Van Driesche & Bellows, 1996).

The success of a natural enemy introduction depends partly on the similarity of the climate in the area-of-introduction

compared with that of the area-of-origin (Franz, 1964; Greathead, 1971). For example, the ladybird *Chilocorus nigritus* (F.) (Coleoptera: Coccinellidae) area-of-origin and areas-of-establishment corresponded well with Walter & Leith's (1960–67) climatic zoniobiomes I–II (Samways, 1989). However, successful establishment may also be influenced by other factors, biotic and abiotic, as well as climate.

Since the pioneering work of Walter & Leith (1960–67), climatic mapping has developed substantially. Among the newer approaches is the CLIMEX program, which predicts species distributions in relation to climate (Sutherst & Maywald, 1985). CLIMEX can be used to express the favourableness of different localities for a species, or to compare the same location in different years (Sutherst, 1990, 1991).

The program integrates the developmental and distributional response of a species to temperature, moisture and daylength into an Ecoclimatic Index (EI) (Sutherst & Maywald, 1985). The EI predicts the extent to which a location has the potential to support a species, and is a measure of the overall climatic favourability of a location for permanent establishment by a species (Maywald & Sutherst, 1991). The EI is a combination of the Growth Index (GI) and various 'stress indices', which describe the effect of adverse climate on a species (Maywald & Sutherst, 1991). The GI estimates the suitability of the climate for population growth in the favourable season. The TI (Temperature Index) describes the favourableness of temperature for survival of a species over one season. CLIMEX is a useful exploratory analysis for determining the likelihood of establishment of species introduced from one area to another (Sutherst & Maywald, 1985). Our study tests CLIMEX in a global, multispecies, retrospective appraisal, which examines localities and their climates around the world where ladybird species of the genus *Chilocorus* (Coccinellidae) have, or have not, established. This provides an estimate of the extent to which overall climate (as opposed to microclimate, food type and availability, parasitism, landscape type, etc.) determines whether a species can survive in a certain area. It also provides evidence on the extent to which geographical ranges can be accurately modelled in the absence of global climate change.

METHODS

The genus *Chilocorus* comprises about sixty-two species (Korfschefskey, 1932; Sasaji, 1971; Leeper, 1976) (Table 1). The areas-of-origin of each of the species was ascertained from museum specimens in: Albany Museum, Grahamstown, South Africa; Entomology Department, University of Pretoria, South Africa; H. Von Fürsch Collection, Germany; Natural History Museum, London, Britain; South African Museum, Cape Town, South Africa; Transvaal Museum, Pretoria, South Africa; Outspan Citrus Centre, Nelspruit, South Africa; Zoology and Entomology Department, Rhodes University, South Africa.

Information from 206 research papers, notes, reports (published and unpublished) and correspondence with biocontrol workers provided the information on the establishment from deliberate introductions, subsequent natural spread and/or invasions of species with no record of

deliberate introductions (see Table 1 for a summary of key references).

The climates of areas-of-origin *v.* areas-of-introduction were then matched using CLIMEX. The critical value for matching climates of two localities was set at 0.6, with monthly rainfall, temperature and relative humidity (am and pm) being used to determine the similarities in climate of the different areas. This was then compared with information on whether or not species-establishment was successful. For this, the Match Index (MI) (based on climatic suitability) was used to predict the successful establishment of species in different areas. The MI varied from 0 to 1.0, the higher the index the more similar was the climate of the two areas. This was done using the MI facility of CLIMEX, which derives an index by comparing monthly rainfall, average maximum and minimum temperature of one locality to another. Sutherst & Maywald (1990) suggest that 0.6 is the critical value below which an introduction of a species is unlikely to establish permanently.

The CLIMEX Ecoclimatic Indices (EIs) were determined by estimating various climatic parameters relating to maximum and minimum temperatures and total rainfall based on the premise that species development is maximal at these model parameters. Ideally, values should be determined from experimental work on the species. However, as this information was often not available, parameters were based on meteorological conditions of the area of origin. EIs ranged from 0 to 100. Any indices above 75 determined for areas-of-origin were considered here to be a good fit of the model for the species concerned. The assumption was made that species would only establish in localities with climates similar to their own area of origin. Temperature Indices (TIs) were also determined for the species, at particular localities, and were used to indicate the suitability of climate for their continued survival. Establishment was implied if the EI and GI were both 75 or above, and MI was 0.6 or above. Any values below these were considered to be not significant (Maywald & Sutherst, 1991). The higher the EI and GI, the greater the likelihood of establishment.

EIs and GIs for each species were derived initially to match areas-of-origin of the species. The indices for each species were mapped and compared with known areas-of-origin to show deviations from the origins. This was based on the assumption that the areas of origin would have the highest EI. The parameters were adjusted and program re-run several times. After each iteration, the EI and GI for localities in the area-of-origin were graphed until these indices approached values of 75 and above for these localities. The regions where species were introduced were then mapped, and their GI and EI were graphed. These maps and graphs showed the EI and GI for species that were predicted from the model. The favourableness/suitability of a location for species development and survival were determined using the 'match climates' routine of CLIMEX, and the EI were determined for all areas irrespective of whether the introduction was successful. Whether or not CLIMEX correctly predicted establishment of species was then determined. The fact that some species establish at indices lower than 75, means that they are climatically fairly tolerant. The model, however, assumes that all species are equally

Table 1 Species of *Chilocorus*, their areas-of-origin, and the numbers of voucher specimens examined to determine the distributions.

Species	Area-of-origin	Records examined, No of voucher specimens
<i>adustus</i> Weise 1898	West Africa	1
<i>alishanus</i> Sasaji 1968	Taiwan	0
<i>amamensis</i> Kamiya 1959	Ryukyu Islands	0
<i>angolensis</i> Crotch 1874*	Central & southern Africa	98
<i>baileyi</i> Blackburn, 1890 ¹	North-eastern Australia	19
<i>bennigseni</i> Weise 1900	Central East Africa	2
<i>bijugus</i> Mulsant 1853	(see <i>infernalis</i> below)	—
<i>bipustulatus</i> (Linnaeus 1758)*	Europe, Middle East, central Asia, North Africa.	390
<i>bivulnerus</i> Mulsant 1850 (= <i>stigma</i>)	(see <i>stigma</i> below)	—
<i>cacti</i> (Linnaeus 1767)*	Southern N. America, central America, northern S. America, Caribbean Islands	62
<i>calvus</i> Weise 1898	Southern & eastern Africa	21
<i>canariensis</i> Crotch, 1874 ²	Canary Islands	10
<i>cerberus</i> Mulsant 1853	Malaysia, Indonesia, Philippines	11
<i>chalybeatus</i> Gorham 1892	South-eastern China	0
<i>chinensis</i> Miyatake 1970	South-eastern China	0
<i>circumdatus</i> (Gyllenhal 1808)*	India, Malaysia, Indo-China, Indonesia, Sri Lanka	25
<i>coelosimilis</i> Kapur, 1967 ³	Andaman Islands	6
<i>cruentus</i> Gorham 1901	Central & southern Africa	11
<i>discoideus</i> Crotch 1874(= <i>schioedtei</i>)	(see <i>schioedtei</i> below)	—
<i>distigma</i> (Klug 1835)*	Sub-saharan Africa	205
<i>dobrni</i> Mulsant 1850	Western & central Africa	35
<i>elegans</i> Mader 1954	Central & eastern Africa	5
<i>esakii</i> Kamiya 1959	Japan	0
<i>flavidus</i> Blackburn, 1892 ¹	North-western & North-eastern Australia	8
<i>fraternus</i> LeConte 1860	USA, California	7
<i>geminus</i> Zaslavskii 1962	Central Asia	0
<i>gressitti</i> Miyatake 1970	South China	0
<i>haematocephalus</i> Sicard 1909	Madagascar, East Africa	5
<i>hauseri</i> Weise 1895*	North-east India, Burma	44
<i>hexacyclus</i> Smith 1959	Central-southern Canada	0
<i>hupehanus</i> Miyatake 1970	Central China	0
<i>infernalis</i> Mulsant 1853*	Himalaya foothills of Pakistan and India	35
<i>ishigakensis</i> Kamiya 1959	Ryukyu Islands	0
<i>kuwanae</i> Silvestri 1909*	Japan, South-eastern China	7
<i>malasiae</i> Crotch, 1874 ⁴	Papua New Guinea, Melanesia	8
<i>marshalli</i> Gorham, 1901 ⁴	Central-southern Africa	2
<i>matsumuri</i> Miyatake 1985	(uncertain)	—
<i>melanophthalmus</i> Mulsant 1850	Malaysia, Indonesia	9
<i>meridionalis</i> Eichler 1924 (= <i>bipustulatus</i>)	(see <i>bipustulatus</i> below)	—
<i>metallescens</i> Sicard 1909	Madagascar	1
<i>midas</i> (Klug)	Madagascar	4
<i>mikado</i> Lewis 1896	Japan	1
<i>nasicornis</i> Korschefsky, 1944 ¹	Papua New Guinea	6
<i>nigripes</i> Mader 1954	East Africa	25
<i>nigritus</i> (Fabricius 1798)*	Indian subcontinent & FarEast	233
<i>orbis</i> Casey 1890	South-western North America	8
<i>pilosus</i> Sicard 1921	Sao Tomé	14
<i>politus</i> Mulsant 1850*	Eastern India, Malaysia, Indonesia, Réunion	20
<i>quadriguttatus</i> Weise 1888	Central South Africa	2
<i>quadrinaculatus</i> Weise 1910	East-central Africa	22
<i>reinecki</i> Weise 1905	Southern Africa	10
<i>renipustulatus</i> (Scriba 1790)*	Europe, Asia Minor, WesternAsia	113
<i>rubidus</i> Hope 1831	China, Mongolia, Korea, Japan, Pakistan, Nepal, India, eastern Siberia, Celebes	15
<i>rufitarsus</i> Motschulsky 1853	Central & southern China	6
<i>rufithorax</i> Mader 1954	Central & southern West Africa	4

continued

Table 1 continued

Species	Area-of-origin	Records examined, No of voucher specimens
<i>rufoplagiatus</i> Pope 1977	Central Africa	22
<i>schioedtei</i> Mulsant 1850*	Western eastern & central Africa	168
<i>sexguttata</i> Weise 1912	Central & East Africa	9
<i>shirozui</i> Sasaji 1968	Taiwan	0
<i>silvestri</i> Wiese 1913	Central Africa	2
<i>similis</i> L. (= <i>kuwanae</i>)	(see <i>kuwanae</i> above)	—
<i>simoni</i> Sicard 1907	Southern Africa	19
<i>solitus</i> Wiese 1899	Eastern & southern Africa	119
<i>stigma</i> (Say 1835)*	Central, eastern & southern North America	43
<i>takara</i> Nakane & Araki 1959	Ryukyu Islands	0
<i>tibialis</i> Weise 1897	Eastern Africa	5
<i>tricyclus</i> Smith 1959	Central-western North America	0
<i>tumidus</i> Leng 1908	Southern North America	0
<i>wahlbergi</i> Mulsant 1850*	Central, eastern & southern Africa	101

* Species that have been translocated in biocontrol attempts¹ *flavidus*, *baileyi*, *nasicornis* may be the same species.

² *canariensis* may be a subspecies of *renipustulatus*.

³ *coelosimilis* may be a colour variety of another species.

⁴ *marshalli* and *malasiae* may not be *Chilocorus* species.

sensitive to the same climatic tolerance. For the purposes of this study, the critical value was taken to be as high as that derived for the natural distribution of the species (i.e. EI at or above 75), which was the lowest value at which species geographical ranges fitted well.

RESULTS

General trends

The general distribution and number of collection records for each species are shown in Table 1. Data were found to be sufficiently good to model only fifteen of the sixty-two species. Table 2 shows the countries and localities (where known) where the fifteen species have been introduced, as well as showing the predicted Match Indices (MI), Ecoclimatic Indices (EI) and Growth Indices (GI) for each locality.

Table 3 shows the indices derived for each of the fifteen species. Permanent establishment was not always correctly predicted for species based on the CLIMEX model. The original geographical ranges of the fifteen species used in the study are shown in Fig. 1(a),(b). The overlapping and contiguous ranges of different species can be seen. The ranges of some of the species overlap, for example *C. circumdatus* and *C. nigrinus*. The range of *C. distigma* and *C. schioedtei* overlap in Central Africa yet are adjacent along the Ivory Coast and Ghana (Fig. 1a).

Results for individual species

Chilocorus angolensis Crotch

This species occurs naturally in southern and central Africa. The CLIMEX model gave high GI and EI for Nairobi and

Johannesburg (Figs 2 and 3), showing that the model derived for this species was good. Introductions into Bermuda, Ghana and USA failed, even though the GI and EI were above the critical value of 75 (Table 2). However, the MI were zero (Table 2).

Chilocorus bipustulatus (L.)

This species is restricted to the Mediterranean region, occurring as far north as Norfolk in the United Kingdom. The CLIMEX model was a good fit to the data, with most areas of origin having an EI of 80–90. Successful establishment was not always correctly predicted, with the species being predicted to establish in South Africa, yet failing to do so (E.C.G. Bedford, personal communication).

Chilocorus cacti (L.)

This species has been introduced into many countries (Table 2). Although the model was accurately derived, many of the predictions of failure were false, and the species did establish.

Chilocorus circumdatus (Gyllenhal)

Almost all predictions for establishment or failure of this species based on the EI and GI were correct (Table 2). Predictions were only made once several iterations had been completed on species parameters so that the indices were correct for the original distribution of the species.

Chilocorus distigma (Klug)

The model for this species was reliable, but the prediction for establishment was incorrect for Bermuda, although correct for the Mahé (Seychelles) and Port Louis (Mauritius), despite that the MI was zero for these two sites.

Table 2 The fifteen species short-listed for CLIMEX analysis, and the countries and localities (where known) where the species have been deliberately introduced with Match Indices (MI), Ecoclimatic Indices (EI), Growth Indices (GI). Localities marked with an asterisk have been naturally invaded by the species.

Species of <i>Chilocorus</i>	Area of introduction	MI	EI	GI	Establishment ¹	References
<i>C. angolensis</i>	Bermuda	0	76	76	F	Bennett & Hughes (1959)
	Ghana	0	70–76	70–76	F	Anonymous report
	USA (California)	0	57–80	57–80	F	Smith & Flanders (1949)
<i>C. bipustulatus</i>	Australia (Perth)	0.69	65	67	E	Compere (1961)
	Barbados	0	58	70	F	Bennett & Hughes (1959)
	USA (California)	0.69	41–67	41–67	?	Gordon (1985)
	USA (San Diego)	0.69	42	43	?	Gordon (1985)
	USA (Los Angeles)	0.69	61	61	?	Gordon (1985)
	USA (Sacramento)	0.69	42	43	?	Gordon (1985)
	USA (San Francisco)	0.69	56	56	E	Doutt (1954a); Huffaker & Doutt (1965)
	Cook Islands (Aitutaki)	0	1	40	?	Walker & Dietz (1979)
	USA (Oahu)	0	100	100	F	Lai & Funaski (1986)
	Iran (Bushehr)	0.61	55	55	E	Stansly (1984)
	Israel (Gaza)	0	60	60	E	Kehat (1970)
	Israel (Jerusalem)	0	37	38	F	Podoler & Henen (1983)
	Mauritania	0	9–40	9–41	E	de Montaigne & Maoulard (1986)
	Mauritius	0	67	71	E	de Montaigne & Maoulard (1986)
	Niger (Naimey)	0	47	47	F	Stansly (1984)
	Niger (Mt. Bagzan)	0	52	53	E	Stansly (1984)
	South Africa (Brits)	0.68	84	85	?	E.C.G. Bedford (pers. comm.)
South Africa (Rustenberg)	0.68	77	87	F	E.C.G. Bedford (pers. comm.)	
South Africa (Kirkwood)	0.68	77	87	E	T.G. Grout (pers. comm.)	
South Africa (Zebediela)	0.60	72	86	?	Anneck (1969)	
Russia	0.60	12	0	?	Izhevskii (1988)	
<i>C. cacti</i>	Bermuda	0	63	63	E	Bennett & Hughes (1959)
	USA (California)	0	5–10	13–15	F	Swezey (1925)
	Colombia	0	41	41	?	Cock (1985)
	Dominican Republic	0.6	19	67	E	Wolcott (1960)
	Haitii	0	0	45	E	Wolcott (1953)
	USA (Hawaii)	0	35–64	37–66	F	Swezey (1925)
	Hispanolia	0	0	0	E	Wolcott (1960)
	India (Bangalore)	0	29	51	E?	Misra <i>et al.</i> (1984)
	India (Deoria)	0	27	0	E	Misra <i>et al.</i> (1984)
	India (Gorakhpur)	0.69	3–47	3–41	E	Misra <i>et al.</i> (1984)
	India (Uttar Pradesh)	0	21	0	E	Misra <i>et al.</i> (1984)
	Mexico	0.67–0.85	30–31	30–32	F	Swezey (1925)
	Morocco	0	4–28	3–33	E	Hattingh & Samways (unpublished)
	Principe	0	0	1	E	Castel-Branco (1971)
	Puerto Rico	0	0	83	F	Wolcott (1960)
	South Africa (Citrusdal)	0.63–0.65	30	30	E	Hattingh & Samways (unpublished)
	South Africa (Rustenberg)	0.65	30–39	39	E	E.C.G. Bedford (pers. comm.)
	Sri Lanka	0	65	53–67	?	Cock (1985)
	Swaziland	0	65	65	?	Catling (1971)
Trinidad	0	0	59	F	Smith & Flanders (1949)	
<i>C. circumdatus</i>	Australia (Queensland)	0	44–100	47–100	E	Houston (1990); A Beattie (pers. comm.)
	Australia (W. Australia)	0	29–69	21–64	F	Wilson (1960)
	Bermuda	0	100	100	F	Cock (1985)
	USA (S. California)	0	30–31	20–30	?	Rao <i>et al.</i> (1971)
	China (South)	0.72	82–93	80–93	E	Swezey (1925)

continued

Table 2 continued

Species of <i>Chilocorus</i>	Area of introduction	MI	EI	GI	Establishment ¹	References
<i>C. distigma</i>	Cyprus (Morphon)	0	41	43	F	DeBach & Rosen (1976)
	Hawaii (Oahu, Molokai, Maui)	0	87	99	E	Leeper (1976)
	India (Uttar Pradesh, Himachal Pradesh)	0	78–99	78–86	E	Simmonds (1962); Tewari & Tripathi (1979)
	South Africa (Rustenberg)	0	61	58	F	E.C.G. Bedford (pers. comm.)
	South Africa (Zebediela)	0	64–65	56	F	E.C.G. Bedford (pers. comm.)
	Switzerland (Nyon)	0	0	0	?	Simmonds (1962)
	USA (California)	0	23–26	24–34	F	Smith & Flanders (1949)
	India (Tamil Nadu)	0.61–0.74	12–64	12–64	F	Sankaran & Mahadeva (1974)
	Seychelles (Mahé)	0	100	100	E	Vezev-Fitzgerald (1953)
	Mauritius	0	93	93	T	Anonymous (1973)
<i>C. hauseri</i>	Bermuda	0	78	78	F	Cock (1985)
	Australia (W. Australia)	0.61–0.65	4–64	5–64	?	Simmonds (1962)
<i>C. infernalis</i>	Cyprus	0	10	10	F	Rao <i>et al.</i> (1971)
	USA (San Francisco)	0	53	53	F	Rao <i>et al.</i> (1971)
	USA (California)	0.83–0.87	19–40	19–41	F	Rosen & DeBach (1978)
	India (North)	0.67–0.78	61–71	60–70	?	Kapur (1956); Rao <i>et al.</i> (1971)
	Israel	0	0	0	?	Argov & Rossler (1988)
<i>C. kuwanae</i>	South Africa (Northern Province)	0	38–60	38–60	F	T.G. Grout (pers. comm.)
	Switzerland	0	0	0	F	Rao <i>et al.</i> (1971)
	Trinidad	0	79	79	E?	Rao <i>et al.</i> (1971)
	Russia (Batumi)	0	0	28	E	Shenderovskaya (1976)
	Russia	0	0	22–29	E?	Shenderovskaya (1976)
	Bermuda	0	65	65	F	Rao <i>et al.</i> (1971)
	Czechoslovakia	0	1	1	F	Rosen & DeBach (1978)
	USA (Oahu)	0	40	40	F	Swezey (1925)
	India (North)	0	37–55	37–55	F	Thakur <i>et al.</i> (1989)
	Israel	0	2–9	2–9	F	Podoler & Hemen (1983)
	Italy	0	1–6	1–5	F	Greathead & Pope (1977)
	USA (Oregon)	0	2–16	2–14	F	Mitchell & Wright (1967)
	South Africa (Zebediela)	0	16–28	16–28	F	Anneck (1969)
	USA (NE)	0.62–0.65	11–52	11–51	E	Hendrickson <i>et al.</i> (1991)
	USA (Washington, DC)	0	12	12	E	Drea & Carlson (1987); Raupp <i>et al.</i> (1992)
<i>C. nigritus</i>	Russia (Adzhar)	0	31	33	T	Kuznetsov (1987)
	Russia	0	11–18	10–18	F	Izhevskii (1988)
	Agalega Islands	0	0	0	?	Greathead (1971)
	* Seychelles (Aldabra)	0	0	0	E	Hill & Blackmore (1980)
	Argentina (San Miguel de Tucuman)	0	7–32	24–29	?	Samways (1989)
	* Brazil (Pernambuco)	0.61–0.72	100	100	E	Samways (1989)
	Chagos Islands (Diego Garcia)	0.68	0	0	E	Orian (1959)
	* Fiji (Mua-Taveuni)	0	68	68	E	Taylor (1935)
	* Ghana (Cape Coast)	0.64	90	90	E	Samways (1989)
	Guam	0	0	0	E	Davis (1972)
	Hawaii (Oahu)	0	56	55	E	Davis (1972)
	Israel	0	0–11	3–6	?	Argov & Rossler (1988)
	Israel (Rehovot)	0	0–11	0–6	?	Samways (1989)
	* Java	0	89	83	E	Chazeau (1981)
	* Kenya	0	15–81	45–81	E	Greathead (1970); Greathead & Pope (1977)
	* Madagascar	0	31–68	19–61	E	Samways (1989)
	* Mozambique	0	39–72	18–72	E	Samways (1984)

continued

Table 2 continued

Species of <i>Chilocorus</i>	Area of introduction	MI	EI	GI	Establishment ¹	References
	* New Caledonia	0	48	53	E	Samways (1989)
	Oman (Dhofar)	0	0–25	0–26	E	Kinawy (1991)
	* Réunion	0.60	31–68	19–68	E	Chazeau <i>et al.</i> (1974)
	* American Samoa	0.73	0	22	E	Gutierrez (1978)
	Seychelles (Mahé)	0.60	80	81	E	Vesey-Fitzgerald (1953)
	* Society Islands (Tahiti, Huahine)	0.64	86	86	E	Delobel (1978)
	* Solomon Islands (Guadalcanal)	0	15–76	11–76	E	Chazeau (1981)
	* S. Africa (KZNatal, Mpumalanga 800m a.s.l.)	0	11–33	0–9	?	Samways (1984, 1989)
	* S. Africa (E, W Cape, KZNatal, Nkwalini 800m a.s.l.)	0	11–33	0–9	?	Samways (1984, 1989)
	* Swaziland	0	0	11	E	Samways (1984)
	* Tanzania	0.62–0.63	29–84	20–91	E	Greathead & Pope (1977)
	* Togo (Anacho)	0	77–90	77–90	E	Samways (1989)
	Uganda (Central)	0	10–67	24–67	F?	Williams & Greathead (1973)
	USA (California)	0	0	2–3	F	Smith & Flanders (1949)
	USA (Florida)	0	17	42	F	Woglum (1913)
	* Vanuatu (Esperito Santo)	0.65	84	84	E	Chazeau (1981)
	* Zimbabwe	0	18–49	20–30	E	Samways (1984)
<i>C. politus</i>	Indonesia (Bali, Java)	0	78–92	78–92	?	Moutia & Mamet (1946)
	Indonesia (N. Sulawesi)	0	76	76	E	Moutia & Mamet (1946)
	Mauritius	0	100	100	E	Moutia & Mamet (1946)
<i>C. renipustulatus</i>	Russia (Black Sea)	0	53	45	T	Rosen & DeBach (1978)
<i>C. rubidus</i>	Russia (Black Sea)	0.44–0.63	9–28	9–28	T	Rosen & DeBach (1978)
	China	0	19–86	20–86	E	Sun (1986)
	USA (California)	0	13–30	13–30	F	Rosen & DeBach (1978)
	Russia	0	2–69	2–69	F	Izhevskii (1988)
<i>C. schioedtei</i>	India (Bangalore)	0	77	77	F	Walker & Dietz (1979)
	India (Hyderabad)	0	33	61	?	Walker & Dietz (1979)
	India (Jagdapur)	0	54	73	?	Walker & Dietz (1979)
	Kenya (Nairobi)	0	80	92	?	Greathead & Pope (1977)
	Mauritania	0	5–28	0–16	F	de Montaigne & Maouland (1986)
	Mauritius	0	100	100	?	Williams (1971)
	USA (San Diego)	0	0	43	F	Rosen & DeBach (1978)
	Uganda (Kawanda)	0	83–100	83–100	?	Greathead & Pope (1977)
<i>C. stigma</i>	Australia (North, South, Western)	0.65	10–100	10–100	F	Wilson (1960)
	Australia (Western Australia)	0.61	39–100	39–100	F	Wilson (1960)
	Bermuda	0	72	72	F	Bennett & Hughes (1959); Cock (1985)
	Chile	0.71	100	100	F	Rosen & DeBach (1978)
	Hawaii	0	92–99	92–99	F	Swezey (1925)
	Italy (Portici)	0	83–96	83–96	F	Greathead (1976)
	Mauritania (Adrar)	0	0	0	F	Iperti <i>et al.</i> (1970)
	USA (Maryland)	0	77	77	E	DeBoo & Weidhaas (1976)
<i>C. wahlbergi</i>	Seychelles (Mahé)	0	99	99	F	Vesey-Fitzgerald (1953)
	USA (California)	0	46–70	49–71	E	Doutt (1954b)

¹ P=Permanent, T=Temporary, F=Failed.

Table 3 The derived Ecoclimate Indices (EI) and Growth Indices (GI) for fifteen *Chilocorus* species

<i>Chilocorus</i> species	EI for best fit to model	GI for best fit to model
<i>C. angolensis</i>	80	74
<i>C. bipustulatus</i>	80–90	80–90
<i>C. cacti</i>	75	75
<i>C. circumdatus</i>	85–100	96–100
<i>C. distigma</i>	100	100
<i>C. hauseri</i>	77	77
<i>C. infernalis</i>	76–77	77
<i>C. kuwanae</i>	75	75
<i>C. nigritus</i>	90–96	90
<i>C. politus</i>	100	100
<i>C. renipustulatus</i>	90	90
<i>C. rubidus</i>	100	100
<i>C. schioedtei</i>	100	100
<i>C. stigma</i>	75–88	75–80
<i>C. wahlbergi</i>	98–100	98–100

Chilocorus hauseri Wiese

The model was accurate as shown by the EI and GI for Darjeeling (India), which is an important area-of-origin for this species (Fig. 4). Most predictions for the failure of the species to establish were correct for the USA and Cyprus. There are few places where the species could become established, although the climate of Cairns, Coff's Harbour and Lord Howe Island (Australia) are very similar to the areas-of-origin.

Chilocorus infernalis Mulsant

The model was reliable, with the EI and GI both having a value of 77 for Srinagar (India). In contrast, the EI and GI derived by the model for southern California suggest failure (which was the case), being very much below 75.

Chilocorus kuwanae Silvestri

This species occurs naturally in Japan and other areas of eastern Asia. Most of the predictions for the failure of this species to become established were correct (Table 2). This was not surprising as there were very few other regions in the world that climatically matched the area-of-origin. Among them were Miami (USA), Rio de Janeiro (Brazil), Port Vila (Vanuatu) and Jayapura (Irian Jaya). This also suggests a low likelihood of establishment in many regions (Table 2).

Chilocorus nigritus (Fabricius)

Although this species was successfully introduced into Mauritius, from where it spread to other islands and Africa, it is indigenous to Asia, and so the parameters were derived with the best fit to localities in Asia. Parameters derived for the distribution of this species fitted well with the EI and GI for Madurai (India) (96 and 90, respectively) and for Bangkok (Thailand) (90 and 90, respectively). This species survives a range of climatic conditions, and so predictions fitted with many localities where the species was introduced and became established. Although there has been interest in establishing *C. nigritus* against *Aonidiella aurantii* (Maskell) in Israel, the EI

that have been predicted are very low (Table 2), suggesting that establishment will not be achieved.

The species has invaded parts of Africa, and Fig. 5 shows that there are many suitable areas for it. Indeed it has been introduced into, and has naturally invaded, many different climatically appropriate regions of the world (Fig. 6). For example, it has naturally invaded parts of South America (e.g. Pernambuco, Brazil) which have a climate similar to that of its home area in India. The climate of Fiji, where the species naturally invaded, also matches parts of its home area in Asia. Figure 7 shows parts of South Africa that are suitable for it, which matches its current distribution in the region (Samways, 1989).

Chilocorus politus Mulsant

Establishment of this species was correctly predicted for the south-eastern parts of Asia and Mauritius. There were many areas in Asia, beyond its south-eastern Asian area-of-origin, that are climatically suitable for this species.

Chilocorus renipustulatus (Scriba)

Predictions for this species establishing just north of the Black Sea were accurate in terms of the MI, EI and GI. Although the climate was favourable for this species, the overall favourability, including stress indices, suggested that permanent establishment was unlikely. The EI ranged from only 9–24, even though the climate was similar to Turkey, where the species occurs naturally.

Chilocorus rubidus Hope

With the notable exception of China, most of the introductions of this species have failed to establish. This concurs with the predictions based on the MI, EI and GI (Table 2).

Chilocorus schioedtei Mulsant

After several iterations, the model parameters derived for this species fitted well with the original distribution of the species, such that the EI and GI were high for parts of Kenya and Uganda where this species occurs naturally. Reliable predictions could therefore be made for this species. However, information is lacking on whether the species has or has not become established in certain areas, particularly Mauritius (Table 2).

Chilocorus stigma (Say)

This species is widespread in North America, partly as it has been introduced across the USA. Many regions in the USA have climates suitable for it (Fig. 8). *C. stigma* has been introduced into many countries, but has failed to establish. Despite a GI and EI both of 100 and an MI of 0–71 (Table 2), it failed to establish at Antofagasta, Chile.

Chilocorus wahlbergi Mulsant

The model derived for this species also fitted well with the original distribution of the species, with EI and GI of area-of-origin varying from 98 to 100. The prediction for the establishment of this species in southern California was correct, although establishment on Mahé, Seychelles was not (Table 2).

Table 4 shows the areas-of-introduction and the predicted

Table 4 Percentage of predictions based on the EI index that were correct for each of the fifteen species of *Chilocorus*

<i>Chilocorus</i> species	EI for best fit to model	GI for best fit to model	%Correct predictions based on EI and GI of 75
<i>C. angolensis</i>	80	74	0
<i>C. bipustulatus</i>	80–90	80–90	33
<i>C. cacti</i>	75	75	35
<i>C. circumdatus</i>	85–100	96–100	89
<i>C. distigma</i>	100	100	80
<i>C. hauseri</i>	77	77	100
<i>C. infernalis</i>	76–77	77	75
<i>C. kuwanae</i>	75	75	67
<i>C. nigritus</i>	90–96	90	70
<i>C. politus</i>	100	100	100
<i>C. renipustulatus</i>	90	90	100
<i>C. rubidus</i>	100	100	100
<i>C. schioedtei</i>	100	100	75
<i>C. stigma</i>	75–88	75–80	50
<i>C. wahlbergi</i>	98–100	98–100	50

MI, EI and GI of each area. Table 2 shows the indices derived for each species, and the percentage correct predictions of establishment. Predictions were correct for only four out of fifteen species, with five predictions being 50% or less.

DISCUSSION

Predictive capability of CLIMEX relative to interrelated abiotic and biotic factors

The models for individual species did not always correctly predict the likelihood of establishment of that species in new geographical areas based on the EI value of 75. This suggests that overall climate is not the sole determinant of establishment (Sutherst & Maywald, 1985) and other factors can play a major role.

Phenology relative to weather conditions

The likelihood of species' establishment is greatest when animals are released during a time of year when the climate, host-species population and their own breeding capability is most favourable. *C. bipustulatus* shows a decline in ovogenesis during mid-summer to winter in Israel (Kehat *et al.*, 1970). Yet this species is also known to reach peak numbers in early summer (Mendel *et al.*, 1985), and to be most active from February to November (Halperin *et al.*, 1995). Delayed development and increase in population numbers of this species may be in response to decreased humidity and temperature (Rosen & Gerson, 1965).

Weather conditions

Some species, such as *C. infernalis*, are more tolerant of cold conditions than others (Samways, 1986). This influences the chance of establishment in localities with less than ideal temperatures. *C. bipunctatus* was not active during the year when the weather was adverse (Saharoui, 1994). Similarly, Podoler & Henen (1983), suggested that failure of some *Chilocorus* species to establish may have resulted from high

temperatures at critical times or prolonged cold weather (Henderson & Albrecht, 1988). Correct timing of introductions of biocontrol agents is therefore important for successful establishment.

The distribution of species may also mirror the distribution of certain rainfall zones. The distribution of *C. stigma* and *C. schioedtei*, for instance, follow the 751 and 1500 mm rainfall isohyets in North America and Africa, respectively. Some of the Asian species, such as *C. kuwanae*, *C. infernalis* and *C. hauseri*, did not establish in many areas. This may have been because their phenology is linked to the exceptional seasonal monsoon extremes in rainfall, unique to this particular part of Asia. The natural distribution of these species is very limited, with *C. hauseri* having a very narrow geographical range (Fig. 1b).

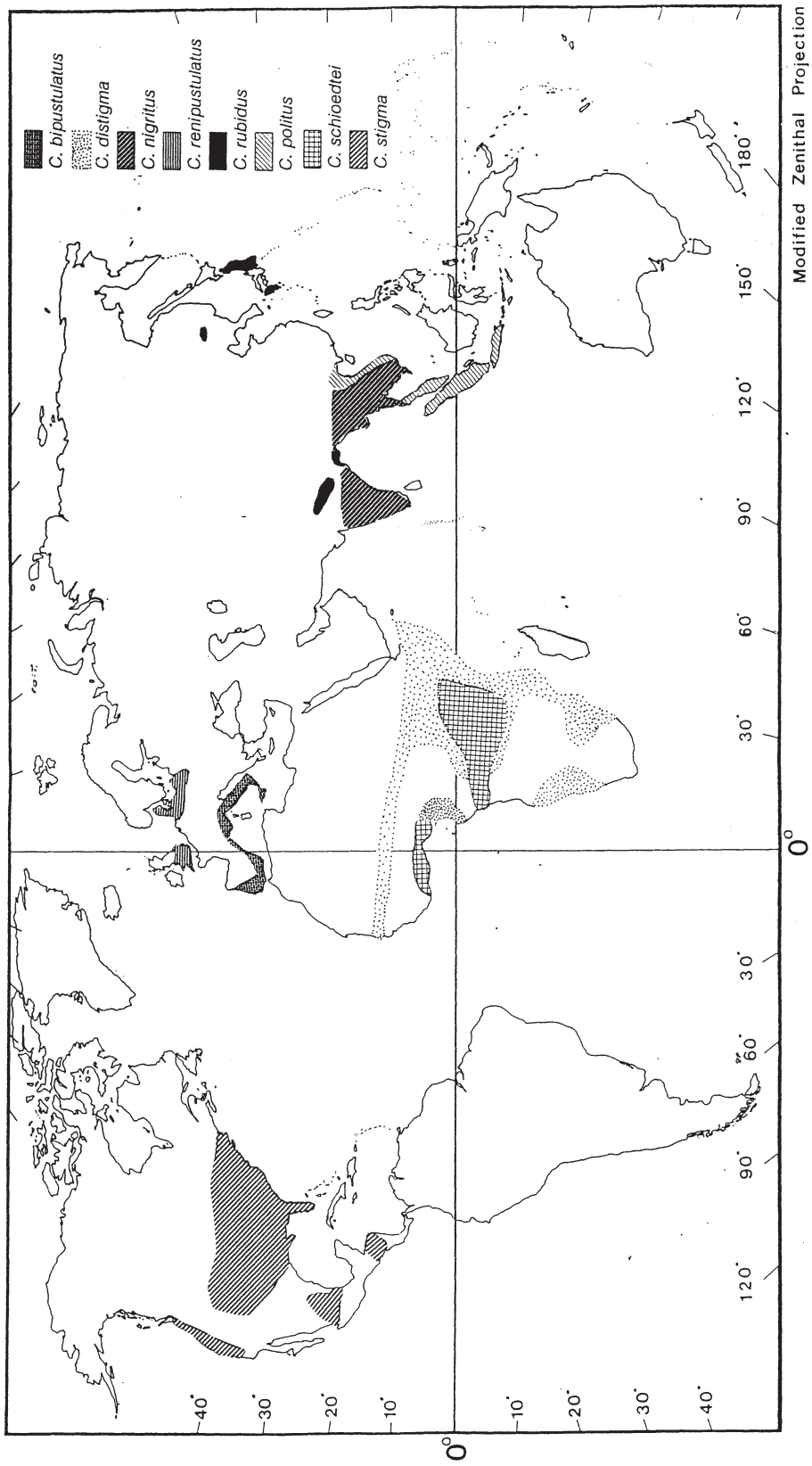
Significance of micro and mesoclimate

Microclimate, topography and elevation are all important for local survival of the species. Elevation can have a profound effect, with as much as a 0.6°C decrease in temperature and 400 mm increase in rain per 1000 m increase (Mielke, 1989). CLIMEX operates on a wider spatial and temporal climatic scale with less emphasis on microclimatic factors such as amount of solar radiation, degree of cloudiness or frequency of wind, all of which are important to a small ectotherm (Unwin & Corbet, 1991). Although climate may appear similar between two sites, other factors such as distance from the sea and elevation can influence local fluctuations in temperatures and rainfall during the year.

The angle of insolation is not the same at different latitudes, and seasonal variations in daylength are greater at high latitudes. This could explain the disparity in distribution of North American species such as *C. cacti* and *C. stigma*, which have not established in other regions of the world (Table 3).

Accuracy of CLIMEX relative to physiological characteristics

The accuracy of the predictions also depends on the preciseness of the physiological parameters derived for the species. This



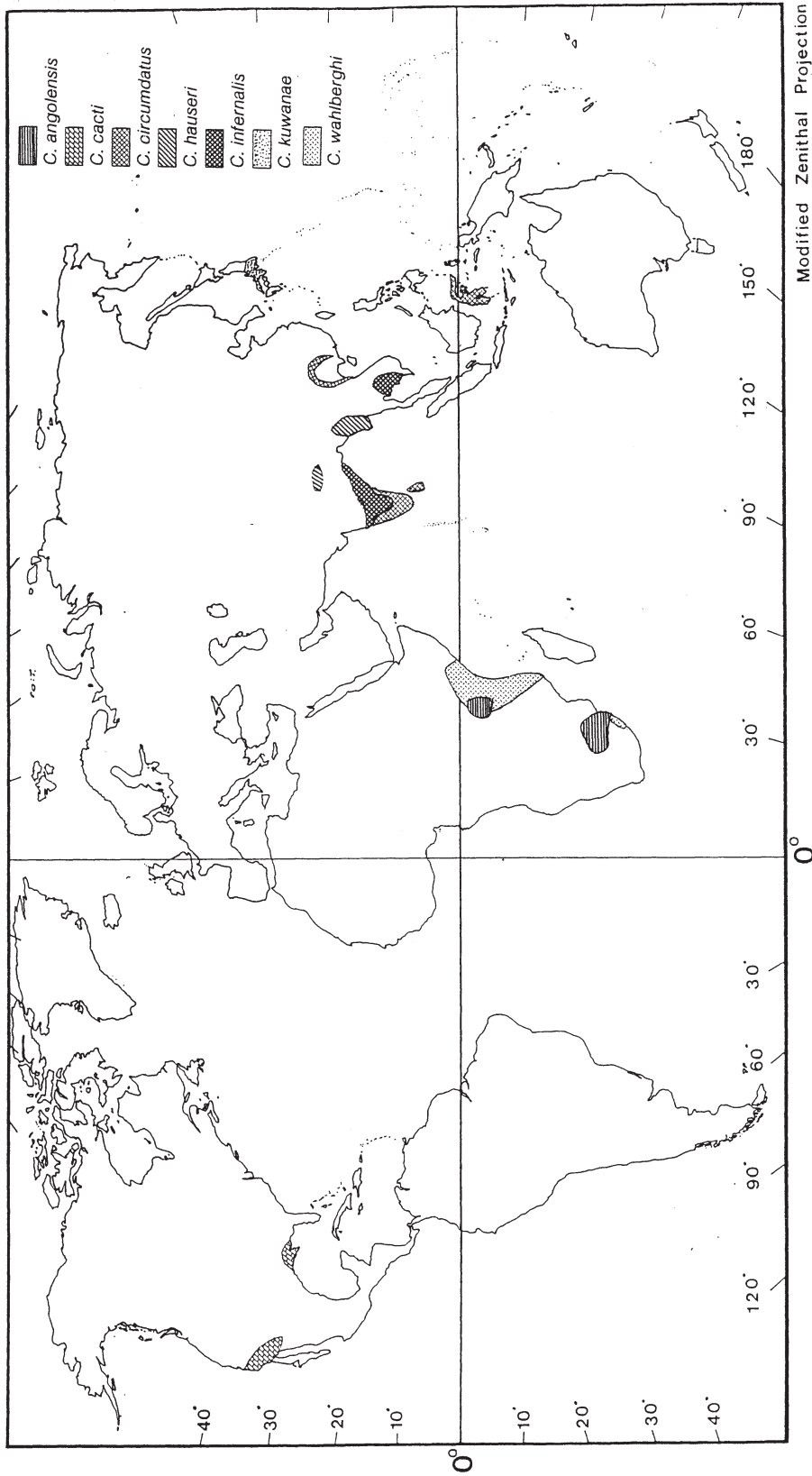


Figure 1 (a) Natural geographical ranges of *C. bipustulatus*, *C. distigma*, *C. nigritus*, *C. renipustulatus*, *C. rubidus*, *C. politus*, *C. schioedtei*, and *C. stigma*. (b) Natural geographical ranges of *C. angolensis*, *C. cacti*, *C. circumdatus*, *C. hauseri*, *C. infernalis*, *C. kuwanae* and *C. wahlbergi*. Areas which have been invaded by species subsequent to introduction are not shown.

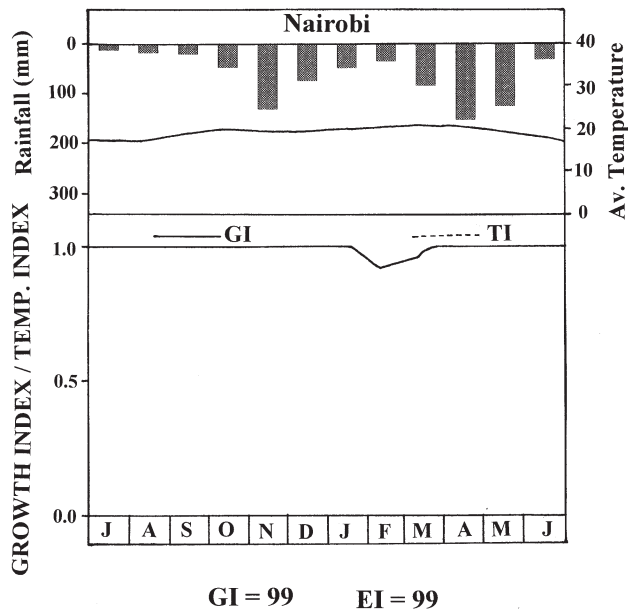


Figure 2 Seasonal values of Growth Indices (GI) and Temperature Indices (TI) for *Chilocorus angolensis* in Nairobi (Kenya). Note that the TI line coincides exactly with GI one. Monthly rainfall and monthly average temperatures are also given. The very high Growth Index (GI) and Ecoclimatic Index (EI) illustrate the accuracy of the model for *Chilocorus angolensis*.

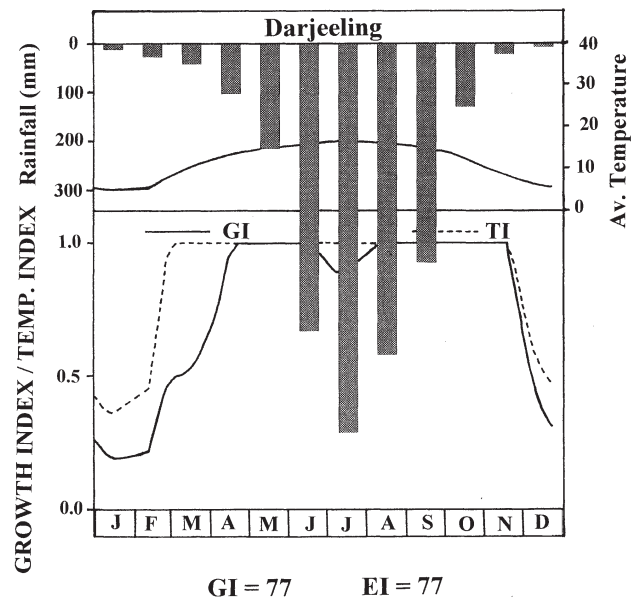


Figure 4 Seasonal values of Growth Indices (GI) and Temperature Indices (TI) for *Chilocorus hauseri* in Darjeeling (India). Monthly rainfall and average temperature are also given. Note that the GI and TI are maximum or almost maximum during the rainy season. The GI and Ecoclimatic Index (EI) illustrate good fit of the model.

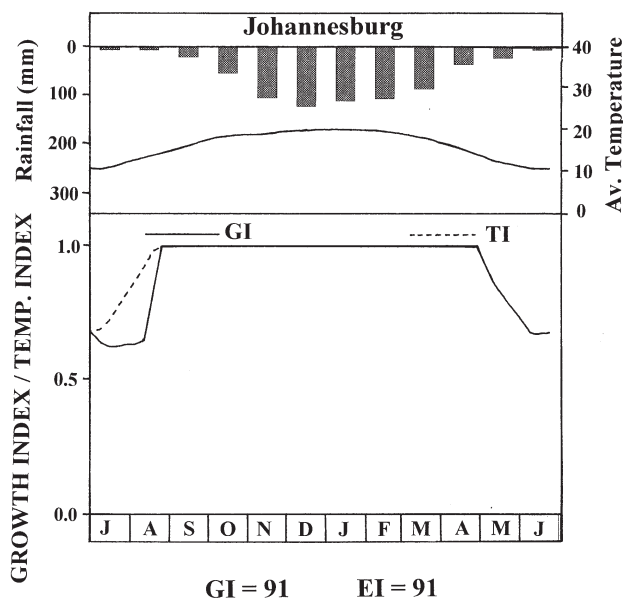


Figure 3 Seasonal values of Growth Indices (GI) and Temperature Indices (TI) for *Chilocorus angolensis* in Johannesburg (South Africa). Monthly rainfall and average temperatures are also given. The high Ecoclimatic Index (EI) and GI illustrate the accuracy of the model for this species.

emphasizes the importance of determining the exact original distribution of the species to accurately derive the parameters and iterate the model until the highest values are obtained. Here, the accuracy of most models was ensured by not performing predictions until the EI and GI for areas-of-origin were between 75 and 100. Nevertheless, even when the model was accurate for the species concerned, CLIMEX predictions of establishment *v.* failure did not always match the actual establishment or failure of the species. Predictions were accurate for species such as *C. hauseri* and *C. politus*, but not accurate for *C. cacti* or *C. bipustulatus* (Table 3). This suggests that adverse climate was not responsible for the establishment failure of *C. cacti* and *C. bipustulatus*. Yet high temperatures do not impair fecundity or survival of *C. bipustulatus* (Applebaum *et al.*, 1971). CLIMEX works on climate being the most important factor determining establishment. It is thus useful in enabling climate to be eliminated as a cause of unsuccessful establishment.

The accuracy and validity of the CLIMEX model is improved where there are experimental data on the optimum temperatures and relative humidities for development of the species. This information provides a more accurate derivation of moisture and temperature parameters. Some information on developmental conditions was available for *C. bipustulatus* (Kehat *et al.*, 1970; Hattingh & Samways, 1994), *C. cacti*, *C. infernalis*, *C. distigma* (Hattingh & Samways, 1994) and *C. nigrinus* (Hattingh & Samways, 1994; Ponsonby & Copland, 1996). We used these in conjunction with the weather conditions of the areas-of-origin in deriving parameters for these species and they gave more accurate predictions (Tables 2 and 4).

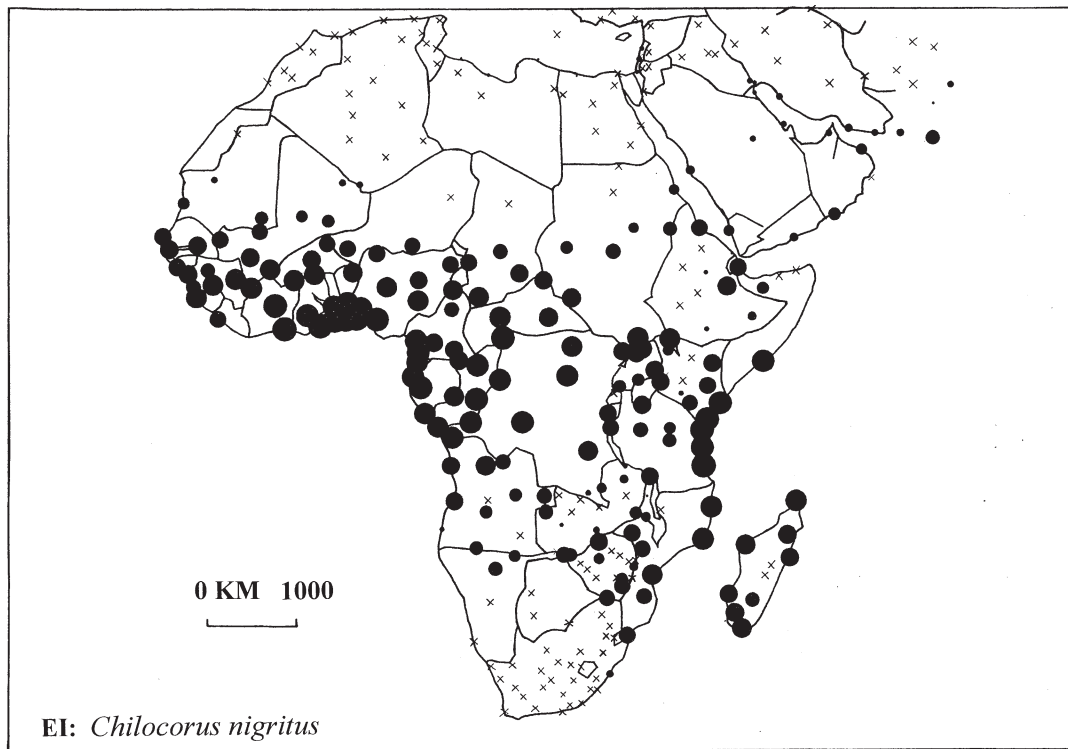


Figure 5 Map of Africa and the Middle East indicating areas of climatic suitability for establishment of *C. nigritus*. Note that Israel is not climatically suitable, and that some parts of Africa are very suitable. The size of the black dots increases in relation to a higher Ecoclimatic Index (EI) and hence suitability of the area for establishment by the species. Largest dots indicate EI=100. Crosses indicate EI=0.

Host availability

In some cases, prediction of establishment based on all three indices was correct. This was the case, for example, for *C. circumdatus* which became established in the south of China (Swezey, 1925), and for *C. bipustulatus*, which became established in parts of South Africa. Where the EI and GI show a high likelihood of establishment, yet the species did not become established, may be because of other biotic as well as abiotic factors. The host may not be the preferred prey of the species, despite laboratory feeding trials to the contrary. Hattingh & Samways (1991), for example, found that *Asterolecanium* sp. was not suitable for *C. infernalis*, while Moutia (1944) suggested that the initial failure of *C. politus* and *C. nigritus* to become established in Mauritius was because the target *Aspidiotus* sp. was not their preferred prey. Although some species are polyphagous, others are more specialized. Some species even require a varied diet, with *C. bipustulatus* unable to rely solely on *Saissetia oleae* (Barnard) (Huffaker & Doutt, 1965). Determination of feeding range is thus important before attempting climate matching. Other biotic factors such as dispersal of individuals and behaviour and interactions with other species may also be important (Sutherst & Maywald, 1985).

Effect of natural enemies

Introduced natural enemies may fail to establish through parasitoid activity (Clausen, 1956). *C. cacti* for example, did

not effectively control the target pest *Aonidiella aurantii* (Maskell) after it was introduced to South Africa, because it was heavily parasitized by an indigenous wasp (Hattingh & Samways, unpublished). The presence of the ants *Pheidole* sp. and *Linepithema humile* (Mayr) in Bermuda were also thought to be the cause of reduced population numbers of *C. angolensis*, resulting in the failure of this species to become established despite favourable weather conditions (Bennett & Hughes, 1959). Similarly, *C. distigma* populations were suppressed by *Pheidole megacephala* (F.) in South Africa (Bedford, 1968).

Size of introduced populations

The number of individuals initially released can be important in determining establishment of a species. *C. cacti* initially failed to establish in Bermuda, but did so after further releases (Bennett & Hughes, 1959). Similarly, *C. distigma* may have failed to establish in Mauritius at first because an insufficient number of individuals were released (Anonymous, 1973). Failure of this species to establish was not due to adverse climate judging by the EI and GI of 93.

Other factors affecting establishment

The migratory habits of a species and heavy insecticide use could also be why a species establishes temporarily (Huffaker & Doutt, 1965). Similarly, unfavourable conditions can cause species to migrate. For example, coccinellids in Algeria moved away to hibernation sites when the climate became

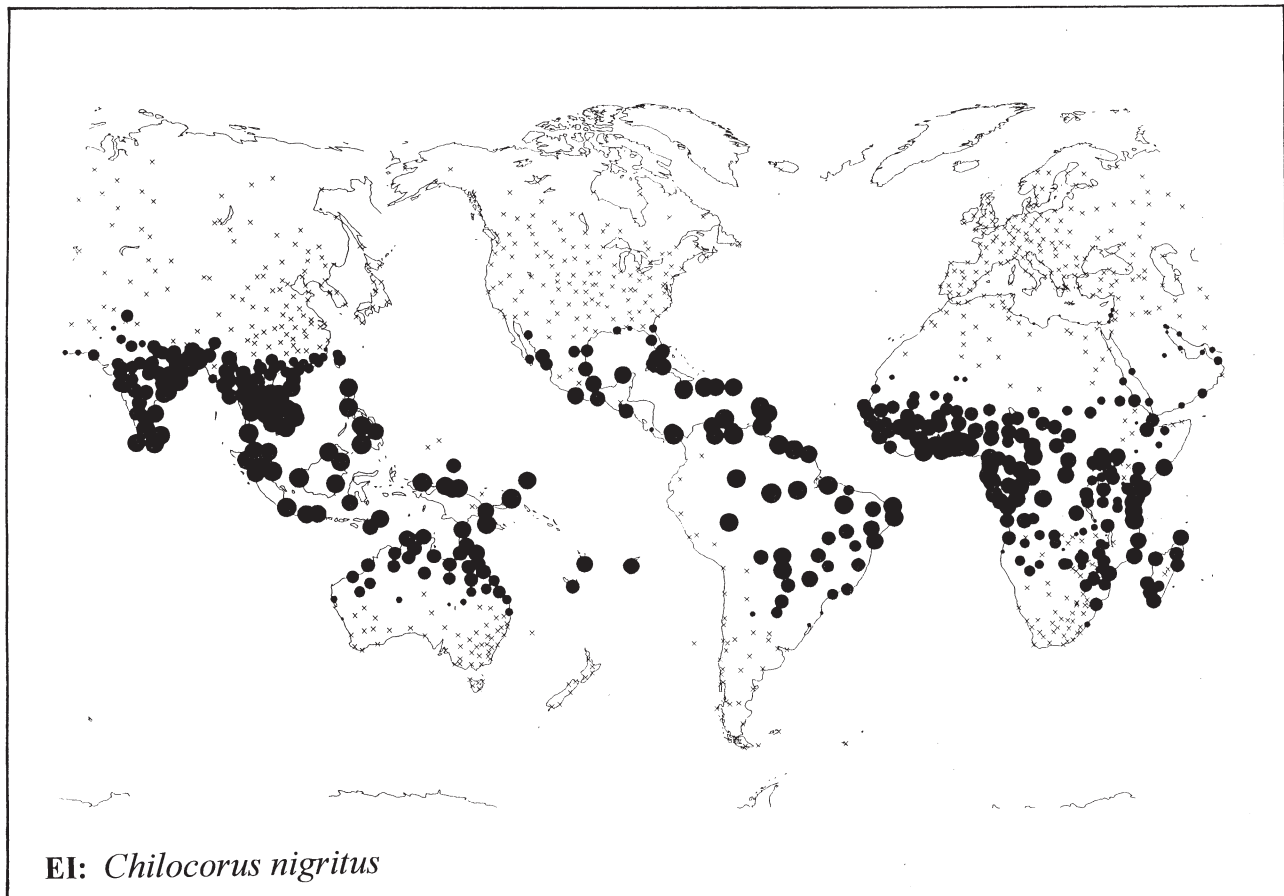


Figure 6 Map of the world showing the many regions where *Chilocorus nigritus* could become established or invade. Most regions are in the low latitudes, stretching from the equator to about 27 degrees north and south of the equator. The greater black dot size indicates increased favourability of the location (i.e. the Ecoclimatic Index (EI) index). Largest dots indicate EI=100. Crosses indicate EI=0.

unfavourable (Saharoui, 1994). A change in weather can also induce aggregation and diapause in *Chilocorus* spp. (Hattingh & Samways, 1995).

Risks of biocontrol

These results illustrate that it is overly simplistic to predict the extent to which a species geographical range will move in the advent of global climate change without knowledge of its biology. This is because for most species, with few exceptions (Hattingh & Samways, 1995), overall climate is not the sole determinant of their geographical location. It was only possible to reach this conclusion from the extensive biological control introductions that have taken place over the last century. Biological control carries inherent risks to nontargets (Howarth, 1991; Samways, 1997) and is currently being much more carefully monitored than in the past. These risks are emphasized here as there is a huge number of subtle biological factors that compound and enhance these risks.

Accuracy of climatic indices

One of the problems in this study was determination of the exact locale of introduction from the literature. This made it

more difficult to use the indices, because the MI, EI and GI sometimes varied greatly within one country, or even in one region of a country. This meant that a range of values had to be used when trying to assess climatic favourability of the region. In some cases, e.g. *C. circumdatus* in Queensland, Australia, the species may or may not establish depending on exactly where the species is introduced. This is because the climatic favourability varies from one exact location to another. The validity of the EI index was difficult to gauge for this species, because the exact location was not specified and it did not establish in Queensland (Houston, 1990). Nevertheless, CLIMEX accurately predicted, in almost half the species we considered, when there was going to be (i.e. there *was*) successful establishment. Indeed, some of the species were overridingly influenced by climatic conditions, such that their establishment could be predicted. Other species may have been influenced more by other factors than by climate, in these cases the results from the model may be useful in indicating other biotic causes. On the other hand, many have a high tolerance to various climates (Greathead, 1989), making correct predictions uncertain. *C. bipustulatus*, for instance, develops in a range of humidities (Nadel & Biron, 1964), which may be the reason for the low level of prediction for this species.

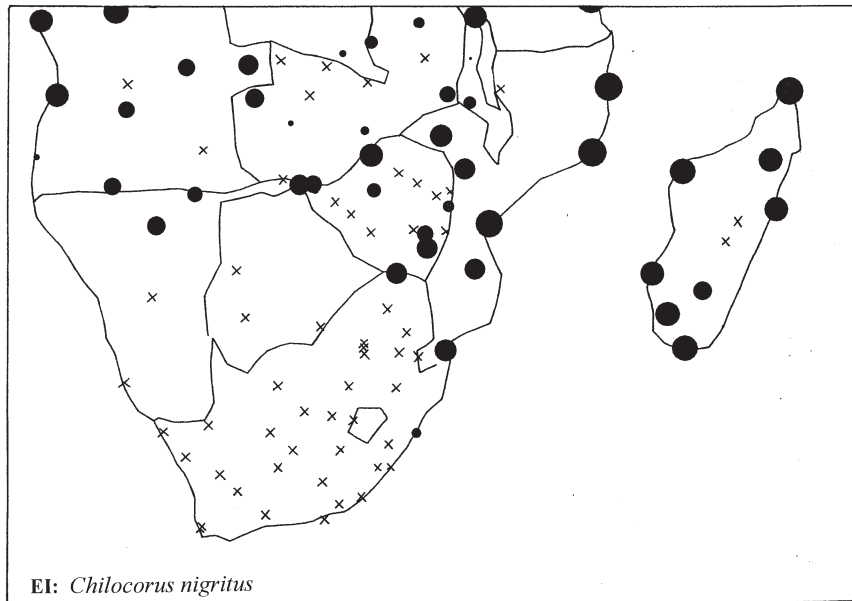


Figure 7 Map showing parts of southern Africa and Madagascar where *Chilocorus nigratus* could, and has in some cases, become established. Increased dot size indicates greater EI.

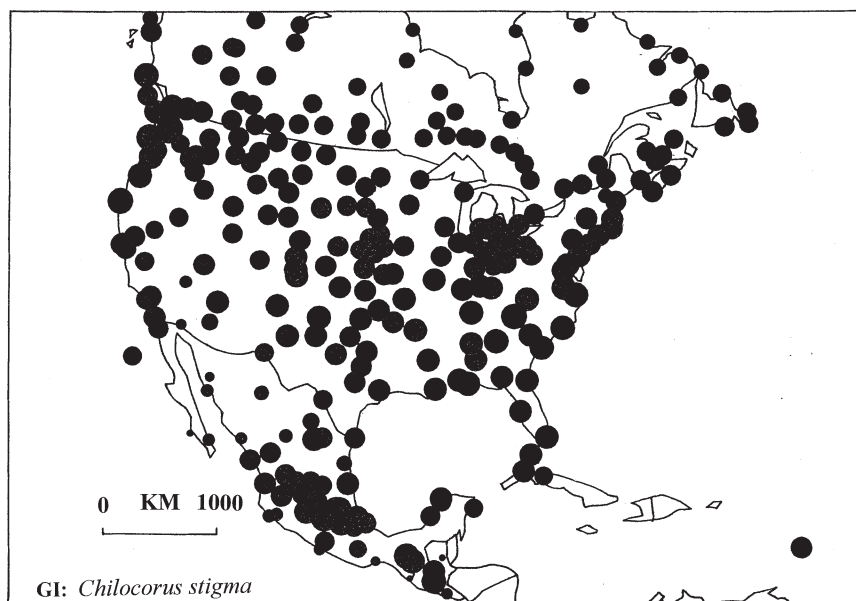


Figure 8 Map of North America showing the favourability of different regions for growth by *Chilocorus stigma* during the favourable season. Dot size increases in relation to favourability of area of growth.

Despite limitations of CLIMEX, it is very useful for estimating climatically suitable areas for biocontrol introductions, for estimating the effect of climate on invasions by exotic pests and weeds, and for conservation decisions. CLIMEX can also be used to show the response of a species to climate during different months of the year in any locations in the world. Sutherst *et al.* (1995) point out it therefore provides a better interpretation of data than conventional analyses such as multivariate statistics and agroclimatic

zonation. This assumes that the biological details of species and the exact climatic preferences are already known.

Since CLIMEX relies on the assumption that climate is the most important, or only, determinant of species establishment, and does not recognize other factors as being important, or take into account, climate tolerance, it cannot accurately predict the geographical range of several species together, even if there are data available on original distribution, and climatic preferences for each of the species.

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