

Including species interactions in risk assessments for global change

R. W. SUTHERST¹, G. F. MAYWALD and A. S. BOURNE

CSIRO Entomology, Long Pocket Laboratories 120 Meiers Rd Indooroopilly, Queensland 4068, Australia

Abstract

Most ecological risk assessments for global change are restricted to the effects of trends in climate or atmospheric carbon dioxide. In order to move beyond investigation of the effects of climate alone, the CLIMEX™ model was extended to investigate the effects of species interactions, in the same or different trophic levels, along environmental gradients on a geographical scale. Specific needs that were revealed during the investigations include: better treatment of the effects of temporal and spatial climatic variation; elucidation of the nature of boundaries of species ranges; data to quantify the role of species traits in interspecies interactions; integrated observational, experimental, and modelling studies on mechanisms of species interactions along environmental gradients; and high-resolution global environmental datasets. Greater acknowledgement of the shared limitations of simplified models and experimental studies is also needed. Above all, use of the scientific method to understand representative species ranges is essential. This requires the use of mechanistic approaches capable of progressive enhancement.

Keywords: *Bactrocera*, biotic resistance, *Boophilus*, *Ceratitis*, climate change, competition, environmental gradients, facilitation, integration, invasive species, predation

Received 2 December 2004; revised version received 13 July 2005 and accepted 19 July 2005

'Far better an approximate answer to the right question which is often vague, than an exact answer to the wrong question which can always be made precise.'

J. W. Tukey

Introduction

Most ecological risk assessments for global change are restricted to evaluating the effects of incremental changes in climatic averages and carbon dioxide (CO₂) on biological processes, phenology, and geographical distributions of species (Walker *et al.*, 1999). This emphasis suggests that climate change and CO₂ are the most important global change threats to biodiversity and agriculture. Without underestimating the importance of climate change, there are other pressing drivers of global change, which need to be addressed effectively on a global scale. This need has been recognized in the Convention on Biological Diversity (CBD), and the establishment of the Global Invasive Species Programme (GISP). These add to the existing activities of the International Plant Protection Convention (IPPC),

Intergovernmental Panel on Climate Change (IPCC), and World Organization for Animal Health (OIE). There is also the need to address interactive effects between different global change drivers (Walker & Steffen, 1999).

There appears to be a consensus on the information needs for assessments of the vulnerability of ecological systems but not on the most appropriate research approaches and methods in this complex field. Standards for pest risk assessments have been developed for trade through the World Trade Organization (WTO) and IPPC. These provide the best-available framework for combining different methods used in pest risk assessments (Baker *et al.*, 2000; Sutherst, 2000). Species mapping is one of the key methods used. At the regional scale, information on potential changes in the geographical distribution and relative abundance of a species informs regulatory agencies. However, its value in local management has been questioned (Hulme, 2003). Local measures are assisted more by population models that include descriptions of biological processes and attributes of management methods and practices. In practice, comprehensive models can be built for

Correspondence: R. W. Sutherst, e-mail: r.sutherst@uq.edu.au

¹Present address: School of Integrative Biology, University of Queensland, St Lucia 4072, Australia.

only the most compelling reasons due to logistical constraints. Simplified, mechanistic species-mapping and phenology models can provide a useful context within which to interpret plot-scale changes (Sutherst & Maywald, 2005). They are a valuable first-step in any ecological study. As such they are complementary rather than competitive modelling approaches so, in the case of the DYMEX™ and CLIMEX™ modelling software (Sutherst *et al.*, 2004; Maywald *et al.*, 2004a,b) the species mapping and population dynamics models have been integrated to create synergy between them.

Most risk assessments address threats to or from individual species (Sutherst & Maywald, 1985; Busby, 1991; Peterson *et al.*, 2002). This acknowledges species as the unit of evolutionary change. There has been a proliferation of uses of statistical or rule-based models to describe species climate envelopes (e.g. Austin, 1987; Busby, 1991; Walker & Cocks, 1991; Carpenter *et al.*, 1993; Rogers & Randolph, 1993; Austin & Meyers, 1996; Cumming, 2000; Guisan & Zimmermann, 2000; Pearson *et al.*, 2002; Peterson *et al.*, 2002; Pyke & Fischer, 2005). Such descriptive models pattern match the species distribution as precisely as possible, with environmental data such as climate. This can lead to major errors of extrapolation, resulting from overparameterization or selection of inappropriate predictive variables (Sutherst *et al.*, 1995a; Sutherst, 1998; Kriticos & Randall, 2001; Thuiller, 2003). The divergent results threaten the integrity of scientific recommendations targeted at informing policy on climate change (Thomas *et al.*,

2004) and the Millenium Ecosystem Assessment (Mooney *et al.*, 2004).

It is axiomatic that if a model can reliably project species geographical distributions in other, independent regions, it is able to accommodate smaller changes in climate caused by climate change. We believe that numerous examples have demonstrated this capacity of the CLIMEX™ model (Sutherst & Maywald, 1985; Sutherst, 2003; Sutherst *et al.*, 2004). Nevertheless, all available species mapping methods have limitations, (e.g. due to the limits of spatial/temporal resolution in the datasets, the difficulties of incorporating other abiotic and biotic variables, and accommodating seasonal and annual changes in species' ranges). The resources needed to support enhanced risk assessments range from global databases and enhanced algorithms, to scenario generators and provision for local user inputs (Table 1). The difficulties of creating such resources and keeping them up-to-date are self-evident.

Habitats are the templates on which ecological strategies develop (Southwood, 1977; Hill *et al.*, 2001). They are complex and multidimensional and are experienced differently by each species. Habitats have many components that should be included in any global change risk assessment. The minimum list should include changes in land use and land cover (Mooney & Hobbs, 2000); travel, trade, and transport distributing diseases and invasive species (Anonymous, 2002); topography; edaphic characteristics; open water bodies; and nitrogen (Vitousek *et al.*, 1997) and phosphorus (Schlesinger, 1977) fluxes. High-resolution, global databases are

Table 1 Environmental change drivers and the global resources needed to advance species-based risk assessments

	Database (historical data)	Scenarios/methods	Local user inputs
Climate	Averages	Climate change (GCM)	Scenarios
	Variances	Extreme event methods	Sensitivity analysis
	Trends	Microclimate models	
	Extremes	Scenario builders	
Atmospheric gases and pollutants	Greenhouse gases	Species response functions	Scenarios
	Nitrogen and phosphorus deposition	Emphasis on nonlinear responses	Fertilizer use
Habitat	Topography	Microclimate model	Soil types
	Soil attributes	Plant edaphic responses	Vegetation type/cover
	Land use/cover	Canopy structure	Land Use
	Open water	Surface water model and data	Water storage
	Irrigation	Irrigation scenario builder	Irrigation practice
Target species	Species traits	Climatic response models	Local occurrence
	Geographical distributions	Data and models for responses to extreme events	
	Abundance along transects.		
Interacting species	Hazard × Exposure data		
	Species traits	Inferential models	Local species interactions
	Ranges of interacting species by region	Mechanistic models	
	Mechanisms		

needed for each of these variables, with scenarios of future change (Leemans, 1996). We also need functions that relate microclimate to radiation and topography (Nikolov & Zeller, 1992); evaporative cooling to radiation (Kingsolver, 1979); evapotranspiration to soil moisture and CO₂ (Farquhar, 1997); and vegetation type and cover to topography and soils. In practice, most of these variables are excluded or controlled in experimental or modelling studies, making the results of such studies incomplete or even misleading.

The extent to which climate limits the geographical distribution of a species is difficult to answer without extensive field and experimental data. Inference has weaknesses and the data are not rigorous so we need to focus on identifying the key variables and responses rather than the pursuit of precision (Sutherst & Maywald, 2005). Our two decades of experience with pests suggests that species' climatic responses explain ~70% of the variation in *potential* geographical distributions. It is relatively economical to account for this variation using the CLIMEX™ model but costly to explain the rest because it involves the development of extensive databases and use of complex simulation models run with geographical information systems (GIS) (White *et al.*, 2003).

Nonclimatic barriers, such as coastlines and mountain ranges are readily detectable. They and a lack of certain climatic types in a region may prevent full parameterization of a distribution model so we have to accept that the limits of a species' tolerance of particular climatic conditions, such as hot-and-wet, must sometimes remain undefined pending records from other regions (Sutherst *et al.*, 2000). Biotic barriers are more difficult to detect and are discussed below. Protocols have been developed to guide the detection of nonclimatic limits to species ranges (FAO, 1996; Sutherst, 2003). To these, we need to add increased awareness of nonequilibrium ranges of invading species.

Movements of mobile species result in potentially large seasonal fluctuations in perceived geographical distributions (the 'source' and 'sink' phenomenon) (Davis *et al.*, 1998). This is a species data issue and there is a need for more systematic recording of seasonal presence and absence. If the seasonal mobility of the species is known, it is feasible with existing approaches to simulate its seasonal variation in geographical distribution. Currently, CLIMEX™ simulates the extent of the annual extremes of conditions that allow persistence and those that support growth (Fig. 1). It can be used to compare the winter range set by stresses with the potential summer range determined by growth conditions. Seasonal maps could illustrate the pulse of growth and stress across geographical space and so enable discrimination between the suitability of the climate on one hand and dispersal rates on the other as factors determining the rate of seasonal range change. Observed annual variations in geographical distributions are also of interest and were related to rainfall using the CLIMEX™ model (Norval & Perry, 1990).

Few biogeographical studies have incorporated species interactions into risk assessments for invasive species or for global change (Baker *et al.*, 2000). As with the other local effects, there are serious parameterization obstacles to overcome. Options are to address the question at community (Lawton, 2000) or functional group (Voigt *et al.*, 2003) level. However, projection of changes in the distribution of plant and animal communities, which are merely transient assemblages of species, is not consistent with evolutionary theory. There are limits to the number of species that can be addressed at the species level and to how many interacting species can be included in any one model. A pragmatic option is to include suitable caveats when significant interactions are suspected (Baker *et al.*, 2000; Sutherst, 2003). Others are to study species linkages in

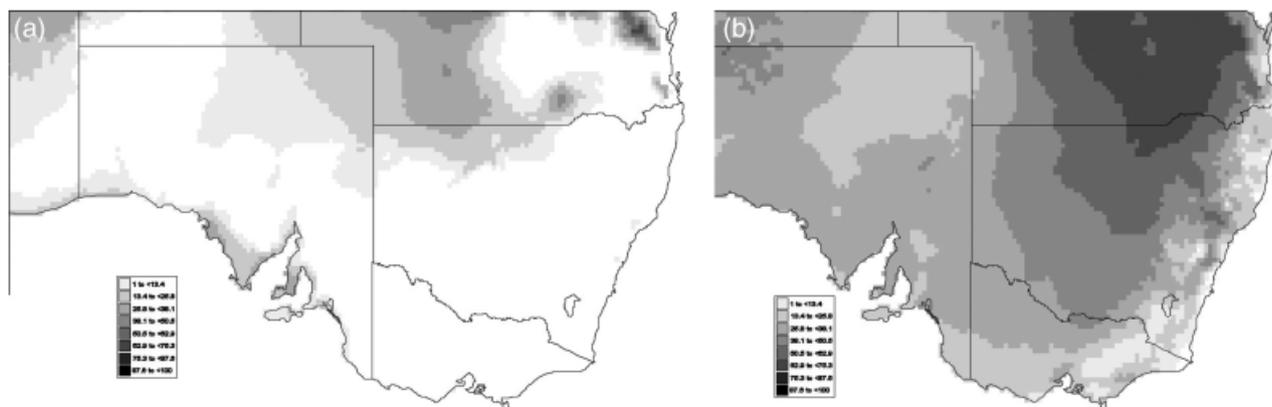


Fig. 1 Seasonal change in the potential range of *Musca vetustissima* in south-eastern Australia using the CLIMEX™ model. (a) Winter range shown by the ecoclimatic index; (b) summer range shown by the annual growth index.

depth with mechanistic models (Sutherst *et al.*, 2000) or food webs (Memmott *et al.*, 1994).

There have been mixed views of the importance of species interactions in determining the abundance and hence geographical distribution of species (Park, 1948; Andrewartha & Birch, 1954; Elton, 1958; Nicholson, 1958; MacArthur, 1972; Davis *et al.*, 1998; Silvertown, 2004). Biological components of habitats include diverse relationships with other species (Damman, 1993) in the same, higher or lower trophic levels. The nature of their effects on the target species vary from beneficial (Bruno *et al.*, 2003) to inhibitory and asymmetrical (Lawton & Hassell, 1981). The relative importance of each component in a habitat differs for different taxa, situation, and scale (Lawton, 2000). Pests, by their very nature, may have fewer interactions with other species than endemic species (Torchin *et al.*, 2003).

The outcome of a species interaction is both species and habitat dependent. Much effort has been put into defining the traits of species which determine their competitive or synergistic capacity (Williamson & Fitter, 1996; Anonymous, 2002). The prospects for defining the attributes of an ecosystem that determine its invasiveness are poor (Williamson, 1996; Anonymous, 2002). Intraspecific competition and niche pre-emption prevent successive colonization by some invasive plant species (Silvertown, 2004). The mediating role of climate in species interactions has also been emphasized (Kingsolver, 1989), while the effects of climate change on trophic interactions and the value of long-term datasets has been recognized (Harrington *et al.*, 1999). The effects of elevated CO₂ on multispecific communities were investigated and it was concluded that subtle changes in structure are more likely than major changes (Navas, 1998).

Detection of the effects of biotic interactions on species' geographical distributions is often difficult under field conditions. We need to detect indirect host- and natural enemy-mediated interactions in addition to climate-mediated competitive or synergistic interactions. Competition may have occurred historically but is not apparent in the current environment (Silvertown, 2004). There is a large literature on the phenomenon of 'biotic release', whereby invaders are highly competitive in new environments when unaccompanied by their predators. Recent examples include (Mitchell & Power, 2003; Siemann & Rogers, 2003; Torchin *et al.*, 2003). Conversely, biological control has often reduced the competitive advantage, and hence, not only the abundance of invasive species, but also their geographical distribution (Bosch van der & Messenger, 1973). These authors also reported the displacement of biological control agents by further agents that were introduced at later times.

Geographical distributions may be truncated in certain directions, with steep ramp- or even a step-shaped declines in abundance at the boundary. The distributions of *Eucalyptus* spp. in south-eastern Australia were asymmetrical and skewed along temperature gradients (Austin *et al.*, 1994). A further symptom of competition is oscillating species composition at a local scale (Wedderburn *et al.*, 1991), which occurs with hybrid zones if either the dispersal rates are high relative to the scale of the observations or climatic variation or host dynamics favour different species in different years (Sutherst, 1987a).

Each of these symptoms points to the action of biological limiting factors. Ecologists need to supplement exclusion experiments (Mitchell & Power, 2003) with analytical methods to detect such cryptic cases of competition. Their interpretation relies on the researchers having a robust climate-response model in which they have sufficient confidence to question apparent inconsistencies in field observations and not just the model. Such issues are inherently geographical in nature and are amenable to solution in part using models such as CLIMEX™ (Sutherst & Maywald, 1985) and STASH (Sykes & Prentice, 2004).

The CLIMEX™ model can sometimes flag strong inter-specific interactions because internal inconsistencies can make it impossible to simulate a truncated geographical distribution (Sutherst & Maywald, 1985). The potential range of *Boophilus microplus* in Africa, estimated using model parameters derived from its geographical distribution in Australia, vastly exceeded the observed range (Sutherst & Maywald, 1985). This pointed to a high-risk situation if cattle movements were increased without adequate sanitary measures to prevent dispersal of the tick (Sutherst, 1987a). The tick has since colonized some of the areas identifiable as being at risk (Sutherst, 2001). Similar results were obtained with fruit flies (Vera *et al.*, 2002) and fire ants (Sutherst & Maywald, 2005).

On the other hand, if the competition is less severe and results in dominance of each species only in their preferred climatic zone, the boundary between them is likely to coincide with a particular zone on a climatic gradient. As such, it may not be possible to isolate the contribution of a species interaction in trimming the potential distribution as determined by climate *per se* without data for each species in isolation. Ultimately, the limits to species ranges need to be defined using combined observational, experimental, and modelling studies.

Recognizing the limitations of current methods of predicting potential geographical distributions under current and future environmental conditions described above, we have investigated the inclusion of species interactions in CLIMEX™. Many of the issues that arose are generic and need to be addressed by the wider ecological communities that are involved with global

change and with invasive species. In order to move CLIMEX™ 'beyond climate' by taking such interactions into account, we have developed new algorithms, which are described below.

Methods

CLIMEX™ is a simulation model of intermediate complexity that is designed to infer species' responses to climate from observations on their geographical distribution and seasonal phenology (Sutherst & Maywald, 1985; Sutherst *et al.*, 1995b; Sutherst, 2003). It addresses situations where process-related data are limited. The model is usually parameterized using ecological observations, but physiological data can be used. The latter are more readily available for growth than for stress parameters, because stress studies can involve prolonged exposure of the target to multiple combinations and permutations of fluctuating and trending environmental conditions, such as low temperature. As with laboratory experiments on species competition (Davis *et al.*, 1998; Jones *et al.*, 1998), extrapolation of physiological data from the laboratory to the field to project accumulation of stress is difficult due to oversimplification of the number of variables and the temporal and spatial variation in natural environments. Field experimentation (Sutherst *et al.*, 1983; Körner, 2000), with close monitoring of environmental conditions and the use of statistical methods to infer response functions (Dallwitz & Higgins, 1978) is a useful additional approach.

CLIMEX™ generates weekly and annual indices of growth and stress in relation to climate and so provides a potential platform for investigating how climate mediates species interactions on regional scales. In the model, growth is described by the following equation:

The weekly (thermo-hydrological), growth index (GI)

$$GI_W = TI_W \times MI_W \times LI_W \times DI_W,$$

where TI_W , MI_W , LI_W , and DI_W are the weekly temperature, moisture, light, and diapause indices, respectively. The DI_W takes into account the effects of day length and temperature on the ability of a species to avoid stress through dormancy or diapause.

Four stress functions (hot, cold, wet, and dry) describe the species' response to extreme values of temperature and moisture. Provision is also made for interactions between the stresses.

The overall response of the species to the climate at any given location is described by the ecoclimatic index (EI), that is scaled between 0 and 100.

$$EI = GI_A \times SI \times SX,$$

where GI_A is the annual growth index, SI is the total stress and SX is the interaction between stresses.

Before we describe algorithms to include further abiotic and biotic environmental variables, we must address the issue of improving our treatment of climate *per se* in order to provide a sound platform for building multivariate risk assessments.

Historical climatic data and climate change scenarios (New *et al.*, 2002) are available at the IPCC Data Distribution Centre (<http://ipcc-ddc.cru.uea.ac.uk/>). The data show a trend of increasing temperatures, but trends in rainfall are very uncertain. The highest current resolution is 10' but digital elevation data are soon to be available at 3 arcseconds with longer-term prospects for 1 arcsecond (<http://www2.jpl.nasa.gov/srtm/>), enabling the creation of global climatic data grids with higher resolutions. High-resolution environmental data reveals topographical features that can have implications for local management. Soil attributes, vegetation cover and open water emerge as issues. For example, a 1.5' climatic grid covering the state of New South Wales in Australia revealed river catchments with significantly higher risks of supporting the cattle tick *B. microplus* in the northern protected area, than 30' or 10' grids, as shown in Fig. 2. The 10' global grid was used in all further simulations. In addition, topography has strong effects on soil moisture balances and surface solar radiation so we need algorithms, data and scenarios to complement the topographical data.

Species mapping models rely on spatial comparisons of climatic averages, and the model parameters are estimated using such data, which contain strong smoothing effects. For example, the 12-year average, winter minimum temperature at New Orleans, USA, is 8.2 °C and the standard deviations based on daily, weekly, and monthly averages are 5.5, 3.4, and 1.5 °C, respectively. The scaling problem of how to relate parameter values derived using long-term average data, to data from successive years need to be resolved to enable the effects of extreme events on potential distributions to be investigated. Time series of species observations are rarely available to reparameterize the models using actual meteorological data.

Global risk assessments rely on long-term average climates and scenarios to provide a baseline for regional comparisons. Errors arise when the regional variances differ greatly (Sutherst *et al.*, 1995). Regions with smaller variances are more benign for species than areas with larger variances with the same means. Differences in variation of temperatures at comparable latitudes in North America and Australia illustrate this problem (Table 2). Similar differences occur in rainfall, with Australia and South Africa having higher variances than continents in the northern hemisphere with similar average rainfall (Peel *et al.*, 2004). Averaged global climate datasets need to include measures of variation at daily, weekly, and monthly timescales. We then need

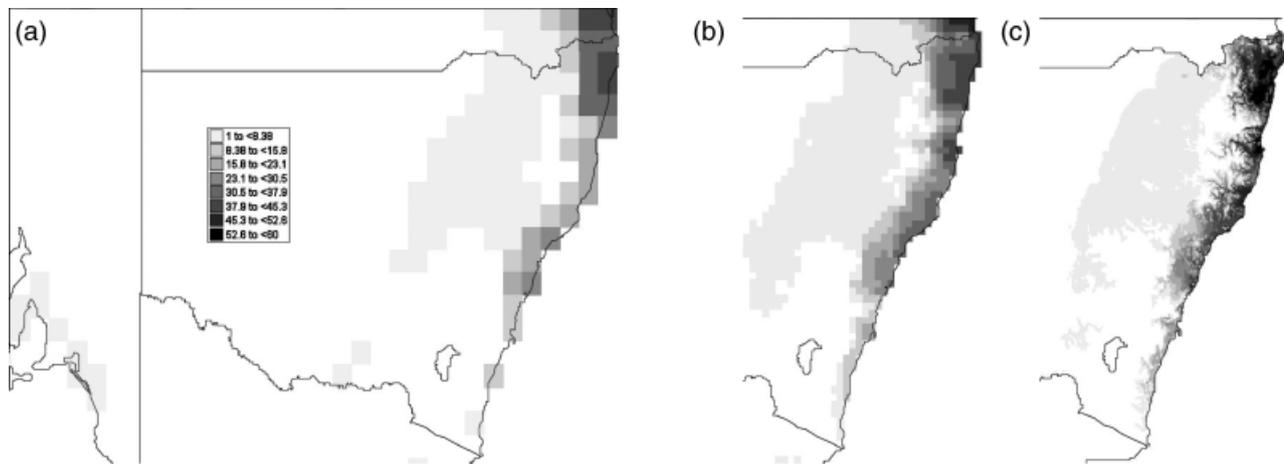


Fig. 2 Comparison of CLIMEX™ EI values for *Boophilus microplus* in New South Wales, Australia showing the effect of changing resolution of climatic average data (a) 30', (b) 10', (c) 90 arc seconds.

Table 2 Comparison of standard deviations (SD) of means of 1970–2000 monthly average January and July temperatures ($^{\circ}\text{C}$) representing winter/summer and summer/winter for three sites in North America and Australia, respectively

Latitude	Longitude	Winter		Summer	
		Minimum ($^{\circ}\text{C}$) (SD)	Maximum ($^{\circ}\text{C}$) (SD)	Minimum ($^{\circ}\text{C}$) (SD)	Maximum ($^{\circ}\text{C}$) (SD)
USA					
37.5	-77.5	-3.3(6.4)	8.3(6.3)	19.6(4.2)	31.4(4.6)
32.5	-117.5	8.4(5.0)	18.3(4.0)	18.0(2.5)	24.6(2.1)
32.5	-87.5	0.8(6.6)	12.6(5.9)	21.3(3.1)	33.2(3.0)
Australia					
-37.8	142	3.1(1.0)	11.1(0.7)	10.8(1.4)	26.6(1.9)
-35.6	149.8	0.3(1.2)	10.6(0.7)	12.0(1.1)	24.8(1.5)
-24.9	152.4	11.1(1.4)	21.9(0.5)	22.0(0.8)	30.5(0.8)

new procedures to take these regional differences in variation into account.

Nonclimatic variables are either abiotic or biotic. In each case, extra model functions and supporting databases are needed to enable their inclusion in an analysis. The increasing concentration of atmospheric CO_2 (Keeling & Whorf, 2004) is an example of such a variable. In order to take the effects of CO_2 and other nonclimatic variables into account, we have introduced a new type of environmental variable into CLIMEX™, called user-defined *Substrates*. Physical substrates can be variables such as CO_2 , soil salinity, or pH. The same form of species response function is used as those for the climatic variables. Substrates can be either constant for all sites or geographically variable. They can also be a seasonal variable. A CO_2 *Substrate* variable can be used not only to describe the hydrological effects of CO_2 but also to describe the fertilization effects on plant growth and on plant–herbivore interactions caused by changes in carbon/nitrogen ratios (Coviella & Trumble, 1999;

Chakraborty & Datta, 2003). The approach to parameterization varies with the available data but can rely on inference from field observations in the first instance. Global data on CO_2 and related greenhouse gases are available (<http://cdiac.esd.ornl.gov/trends/trends.htm>). Ongoing collation of the effects of enhanced CO_2 on weeds, insects, and fungi is needed, taking heed of the need to provide for the nonlinearity of responses (Körner, 2000). Global databases are also available for soils (<http://www.fao.org/CATALOG/new/products/V8600-e.htm>) and land cover (Leemans, 1996). Oceanic temperatures and salinity (<http://www.nodc.noaa.gov/GTSPP/gtspp-home.html>) are available for marine risk assessments.

Full details of the CLIMEX™ model are available in (Sutherst & Maywald, 1985; Sutherst *et al.*, 2004). We have added the following user-definable functions to CLIMEX™ to describe plant and animal species interactions. Plant species reduce the amount of light or water available to each other and their response functions

depend on such factors as growth forms and rooting patterns. The GI now includes a radiation index (RI_W), which describes plant responses to solar radiation. Algorithms describe seasonal variation in solar radiation at any given latitude. Applications of the model can be extended by users to accommodate the effects of local topography on direct radiation (Nikolov & Zeller, 1992). They facilitate investigation of local effects of slope and aspect on flora and fauna, particularly at high latitudes where seasonal solar angles vary so much. Functions allow partitioning of available light and water between competing species with competition reducing the radiation or soil moisture by an amount determined by the GI of the competing species.

A 'raw' plant growth index (TGI_W) is now defined as follows:

$$TGI_W = TI_W \times MI_W \times RI_W \times LI_W \times DI_W,$$

where RI_W is the weekly radiation index.

A species interaction with its biotic resources affects its growth rate relative to another species, so we use one of the user-definable substrate variables to create a *Biological Substrate Index* (BSI_W). This enables CLIMEX™ to model the weekly growth response to a passive biological substrate (e.g. host or nonspecific biotic resistance). The TGI_W now becomes

$$TGI_W = TI_W \times MI_W \times RI_W \times BSI_W \times LI_W \times DI_W.$$

The overall effect is incorporated into the annual measure of relative abundance, the CLIMEX™ EI for each species. An intermediate, 'raw' ecoclimatic index (EI_A) describes the annual species performance including the effects of competition for moisture, radiation, and use of substrates. It is calculated as follows:

$$EI_A = TGI_A \times SI \times SX.$$

A dynamic *Biotic Index* (BI) combines a *Species Interaction* parameter ($SIP0$) with the weekly GI to describe the effect of Species 1 on Species 2 and *vice versa*. The $SIP0$ describes the nature and extent to which species affect each other based on their biological traits. For example, one-on-one, larvae of the tropical fruit fly, *Bactrocera dorsalis*, are more detrimental to survival of larvae of the Mediterranean fruit fly (Medfly), *Ceratitidis capitata*, than *vice versa* (Keiser *et al.*, 1974). The $SIP0$ modifies the weekly growth of Species 1 by adding or subtracting the nominated proportion of the GI of Species 2 to or from the 'raw' weekly GI of Species 1. The weekly *Biotic Index* (BI_W) is defined as follows (Fig. 3):

$$BI_W(1) = 1 + SIP0_1 \times TGI_W(2),$$

$$BI_W(2) = 1 + SIP0_2 \times TGI_W(1),$$

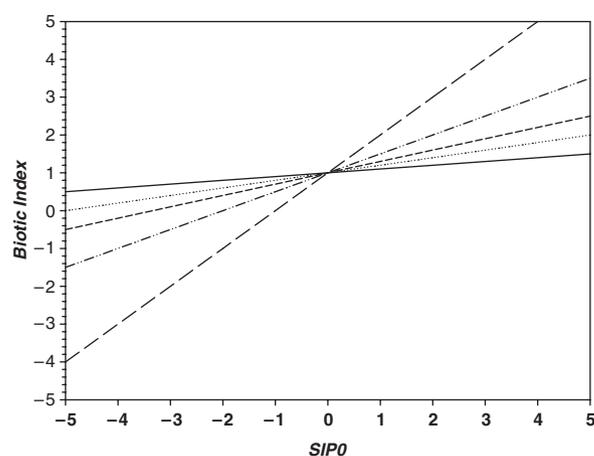


Fig. 3 Values of the CLIMEX™ *Biotic Index* for Species 1 related to its *Species Interaction* parameter ($SIP0$) and the growth index of Species 2. —, $GI = 0.1$; ·····, $GI = 0.2$; ---, $GI = 0.3$; - · - · - ·, $GI = 0.5$; — — —, $GI = 1.0$.

where $SIP0_{1,2}$ are the *Interaction* parameters for Species 1 and 2, respectively. For example, $SIP0_1$ specifies the intensity and direction of the effect of Species 2 on Species 1.

The final weekly growth index, GI_W , then includes the BI_W term

$$GI_W = TGI_W \times BI_W.$$

An extended ecoclimatic index (EI_B) that includes the effects of the BI is calculated as follows:

$$EI_B = GI_A \times SI \times SX.$$

The $SIP0$ is estimated from field observations, using the CLIMEX™ inference paradigm, where the two species have been in contact long enough to produce a stable equilibrium geographical distribution. This can be supported with mechanistic explanations derived from empirical data. Where no prior contact has been made, resort to species traits (Duyck *et al.*, 2004) and experimental studies will be needed to supplement the estimated responses of each species to environmental variables. The size of the native range is an indication of the adaptability of the species (Goodwin *et al.*, 1999) and will be reflected in the CLIMEX™ EI values.

An over-riding exclusion rule is implemented by using a *Competitive Exclusion* parameter, which causes the species with the greater EI to exclude the other species from the location by setting its EI to zero. Each species wins in that environment in which it is most productive. Thus, based on precedents in other regions, it is possible to parameterize the model to simulate competitive exclusion of species, even when the advan-

tage is small but accumulates over time. Displacement has been recorded frequently and includes successive introduced predators (Bosch van der & Messenger, 1973), closely related species that produce less-fit hybrids (Barton & Hewitt, 1989), or less-closely related fruit fly species that compete for fruit (Christenson & Foote, 1960; Vera *et al.*, 2002; Duyck *et al.*, 2004). Exclusion may be rapid (Sutherst, 1987a; Huxel, 1999) or take decades to achieve in the field (Vera *et al.*, 2002).

An ecoclimatic index (EI_C) that includes the *Competitive Exclusion* term is defined as follows:

$$EI_C = EI_B,$$

where the EI_C for the species with the smaller EI_B is reduced to zero.

The effects of a Species 2 on the distribution of a target Species 1 and *vice versa* depend on whether it is in the same trophic level, or above or below it, and on the nature of the specific interaction.

Hosts of host-specific predators, such as herbivores and parasites, constitute a resource that can vary seasonally in availability and suitability across their range. Host ranges may be greater or smaller than the potential range of the predator as determined by climate alone. The relationship between host and predator is mediated by climate, both through direct effects on their relative growth rates but also through effects on the resistance of the host. Rapidly growing host plants can be both attractive and susceptible to herbivore attack (Room *et al.*, 1989). Forest trees, on the other hand, are often made more susceptible to pest attack after drought (Mattson & Haack, 1987). Similarly, animal hosts lose their resistance to parasites when their nutrition is suboptimal (Sutherst, 1987b). Thus, the resources required to investigate likely effects of hosts on ranges of predators include not just presence or absence data, but also the relative suitability of the host for each species and its seasonal variation under different environmental conditions.

As we have seen above, we have two options for incorporating the effects of hosts on the population growth rates of predators in CLIMEX™. In the simplest option, hosts are treated as a passive constant or seasonally variable *Biological Substrate*, which can be exploited differentially by competing predators. Alternatively, a host and a predator can be treated as dynamically interacting species, which have effects on each other through the *Biotic Index*. Both of these functions modify the GI values only, not the stress functions.

Unlike hosts that usually affect feeding of predators most during their growth season, predators can affect the viability of their hosts during both their growth and nongrowth or 'stress' seasons. Therefore, description of interspecific interactions involving predator effects on

hosts ideally need to include the interactive effects on both growth and survival functions. At this point, we have only incorporated the effects on the host population growth rates into CLIMEX™ in the form of a negative *Biotic Index* associated with the predator. It effectively reduces the size of the population that is available to survive through the stressful season.

Interspecific interactions in the same trophic level are most likely to occur during the growth season. They can involve competition for various resources (Davis & Pelsor, 2001) such as water, nutrients, or mates or facilitation by a number of mechanisms (Bruno *et al.*, 2003). CLIMEX™ describes plant competition through differential exploitation of soil moisture, solar radiation and other *Physical* or *Biological Substrates*, resulting in modified population growth of each species. Species displacements of both plants and animals can also occur, based on differences in growth rates as determined by the *Biotic Index* and *Competitive Exclusion* parameter. Each species is affected by its competitor's traits as described by the species couplet-specific *SIP0s*. Facilitation is described in CLIMEX™ model by reversing the sign in the competition function.

Results

Space and the subject of the special issue limit the results reported here to entomological applications. A brief summary of selected results will be followed by detailed case studies to be published elsewhere.

Based on the premise that the area occupied by a species will depend on the balance of births, deaths, immigration, and emigration at each location, the question arises as to how much effect biotic resistance can have on the potential range of a sedentary species. We investigated the intertrophic effect of host resistance on the potential geographical distribution of the tick *B. microplus* in eastern Australia, using the *Biological Substrate* variable. The simulations compare the tick's potential range on cattle breeds with high or low resistance to tick feeding. About 1/6th of the proportion of ticks mature on resistant Asian zebu (*Bos indicus*) cattle (0.025) compared with low resistant European (*Bos taurus*) breeds (0.15) (Utech *et al.*, 1978). Both breeds are used in the Australian beef industry but the dairy industry uses exclusively *B. taurus*. The *Biological Substrate* was set equal to unity for the European breed simulation as a baseline and 0.16 for the zebu simulation. The results (Fig. 4a and b) illustrate how the zebus reduce the potential range and relative abundance in relation to climate throughout. This is in accordance with comparative, field observations that showed mean tick numbers on European and zebu breeds of 465 and five in Central Queensland compared with 302 and 0.5

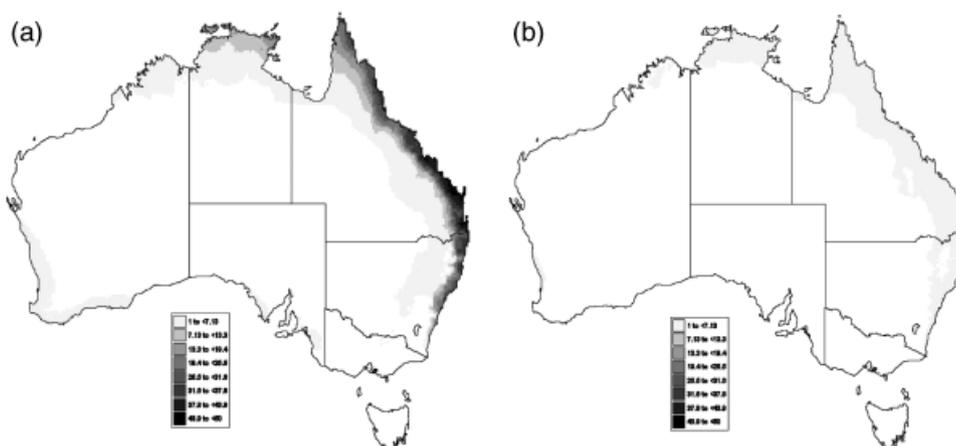


Fig. 4 Simulated geographical distribution of the tick *Boophilus microplus* in Australia with (a) low and (b) high tick resistant cattle.

in cooler southern Queensland, respectively (Bourne *et al.*, 1988).

The regional consequences of intratrophic competitive exclusion of the endemic species of tick, *Boophilus decoloratus*, by the introduced Asian species, *B. microplus*, in sub-Saharan Africa (Sutherst, 1987a) were investigated. The two species infest livestock, but the former is better adapted to wildlife (Norval & Sutherst, 1986) and tolerates drier, cooler climates. *B. microplus* is adapted to cattle (Norval & Sutherst, 1986) and requires hot-humid climates (Howell *et al.*, 1978). The species produce sterile hybrids that form a barrier to invasion of each other's territories. On first introduction to an area, *B. microplus* rapidly displaces *B. decoloratus* because the cattle have not yet acquired resistance to its feeding. Thereafter, there is an unstable equilibrium and the dominant species varies with seasonal conditions in regions where neither has a large advantage and with dispersal rates on moving cattle.

The regions of Africa, that are estimated to be climatically suitable for each species on its own, are shown in Fig. 5a and b. The areas where each species is most likely to dominate when the ticks are placed together are shown in Fig. 5c and d. Mutual exclusion is enforced with the *Competitive Exclusion* parameter allowing the species with the higher *EI* to displace the other. *B. microplus* dominates in hot-humid habitats and *B. decoloratus* in the cooler and drier regions as expected. Differential availability and suitability of the zebu hosts for the two species is described with the *Biological Substrate* ($BSI_{Bm} = 0.02$; $BSI_{Bd} = 0.015$). With this differential *B. decoloratus* is restricted further to those areas with climates to which is best adapted. Under a 2°C climate change scenario and exclusion, *B. microplus* expands its potential range in Central Africa and retreats slightly in the Sahel, while *B. decoloratus* retracts around the hotter edges of its range (Fig. 5e and f).

A plant-herbivore interaction was then investigated. The Queensland fruit fly, *Bactrocera tryoni*, is credited with displacing the Medfly, *C. capitata*, from south-eastern Australia, and there is evidence that it prevented the Medfly's spread into the tropics (Vera *et al.*, 2002). Queensland fruit fly has a more competitive oviposition strategy, resulting in reduced survival of Medfly larvae in mixed infestations. The effect is not reciprocated, giving Queensland fruit fly a comparative advantage. Further, Queensland fruit fly is adapted to warm-humid conditions (Yonow & Sutherst, 1998) while Medfly is adapted to temperate and Mediterranean climates (Vera *et al.*, 2002). Thus, we would expect Queensland fruit fly to have an advantage in the warm coastal habitats in eastern Australia, particularly where irrigation is used, and Medfly to have an advantage in the temperate climates of southern and western Australia. CLIMEX™ models have already been built for the two species (Yonow & Sutherst, 1998) and (Fig. 6a), (Vera *et al.*, 2002) and (Fig. 6b). We investigated conditions that allowed the displacement of Medfly in accord with historical field observations but including irrigation. Firstly, we applied 30 mm of irrigation per week as top-up applications in summer to approximate horticultural practices. Occupation is mutually exclusive so we used the *Competitive Exclusion* parameter. Secondly, we used a negative *SIP0* for Medfly ($SIP0 = -2$) to reflect reduced larval survival rates in mixed infestations. The results are shown in Fig. 6c and d. The Medfly was displaced from the wet eastern coast of Australia while it persisted in cooler, drier regions. Under a 2°C scenario Queensland fruit fly becomes as much a southern Australian problem as a wet tropical one, while Medfly is almost displaced from the continent. Simulations for Hawaii gave a similar result to that observed (Keiser *et al.*, 1974), with Medfly being displaced to the cooler high altitude areas by *B. dorsalis* that is a very similar tropical species to

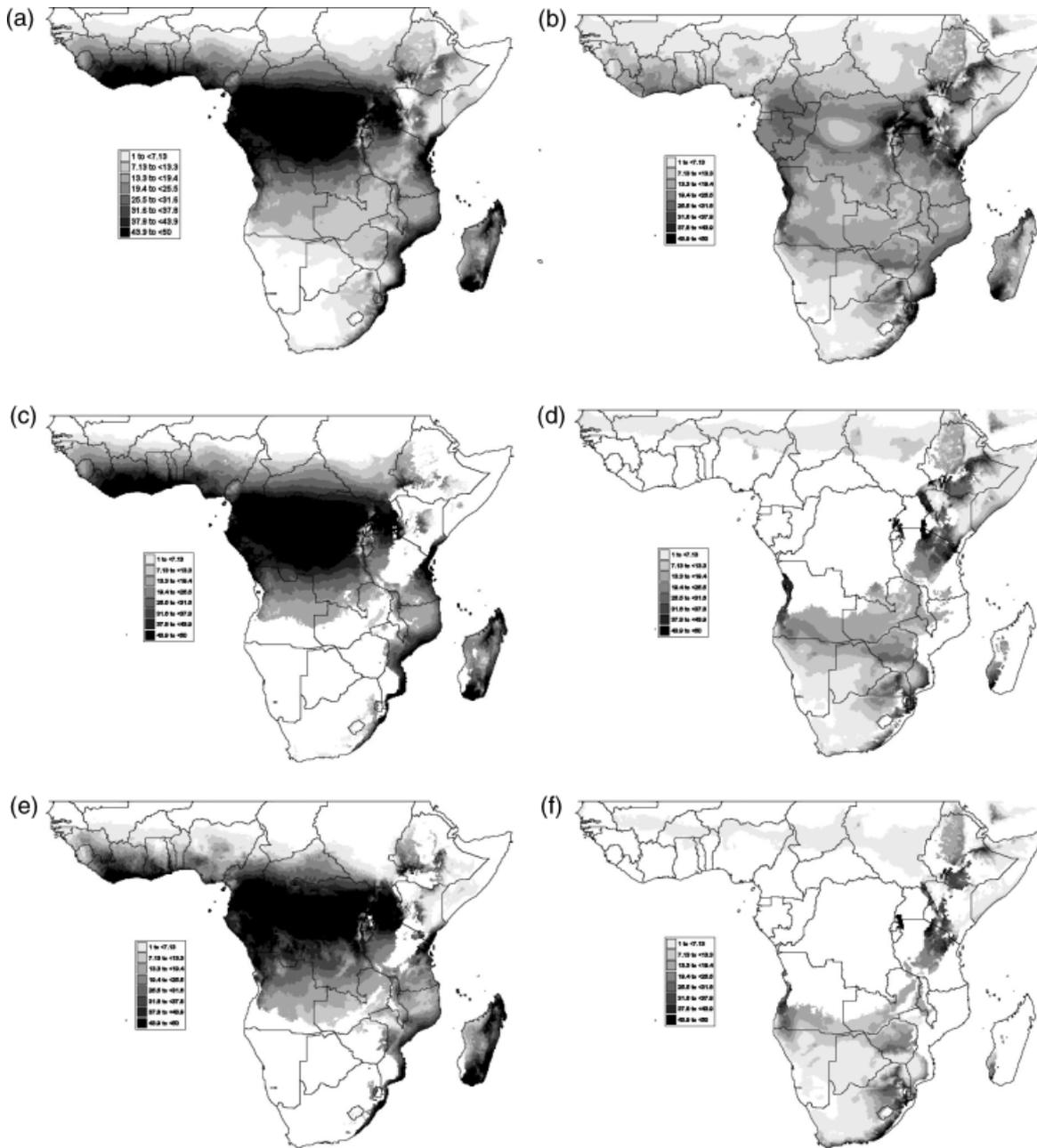


Fig. 5 Potential geographical distributions (CLIMEX™ *ED*) of the livestock ticks, (a) *Boophilus microplus* and (b) *Boophilus decoloratus* in relation to climate in Africa separately; (c) *B. microplus* and (d) *B. decoloratus* when allowed to interact with competitive displacement by the species with the highest annual relative abundance (*ED*); (e) *B. microplus* and (f) *B. decoloratus* with a 2 °C climate change scenario and competitive displacement.

B. tryoni. The relative availability and suitability of hosts for each species, represented by a *Biological Substrate*, changed the balance between the species.

Discussion

Our results demonstrate that it is possible to account for the effects of species traits when investigating interspe-

cific interactions along environmental gradients. The effects of such interactions greatly exceeded the effects of mooted changes in the species' geographical distributions as a result of climate change in the selected systems that we investigated. The results show promise of being able to help fill a major gap in global change risk assessments. We believe that we have demonstrated that trophic levels and mechanisms of species

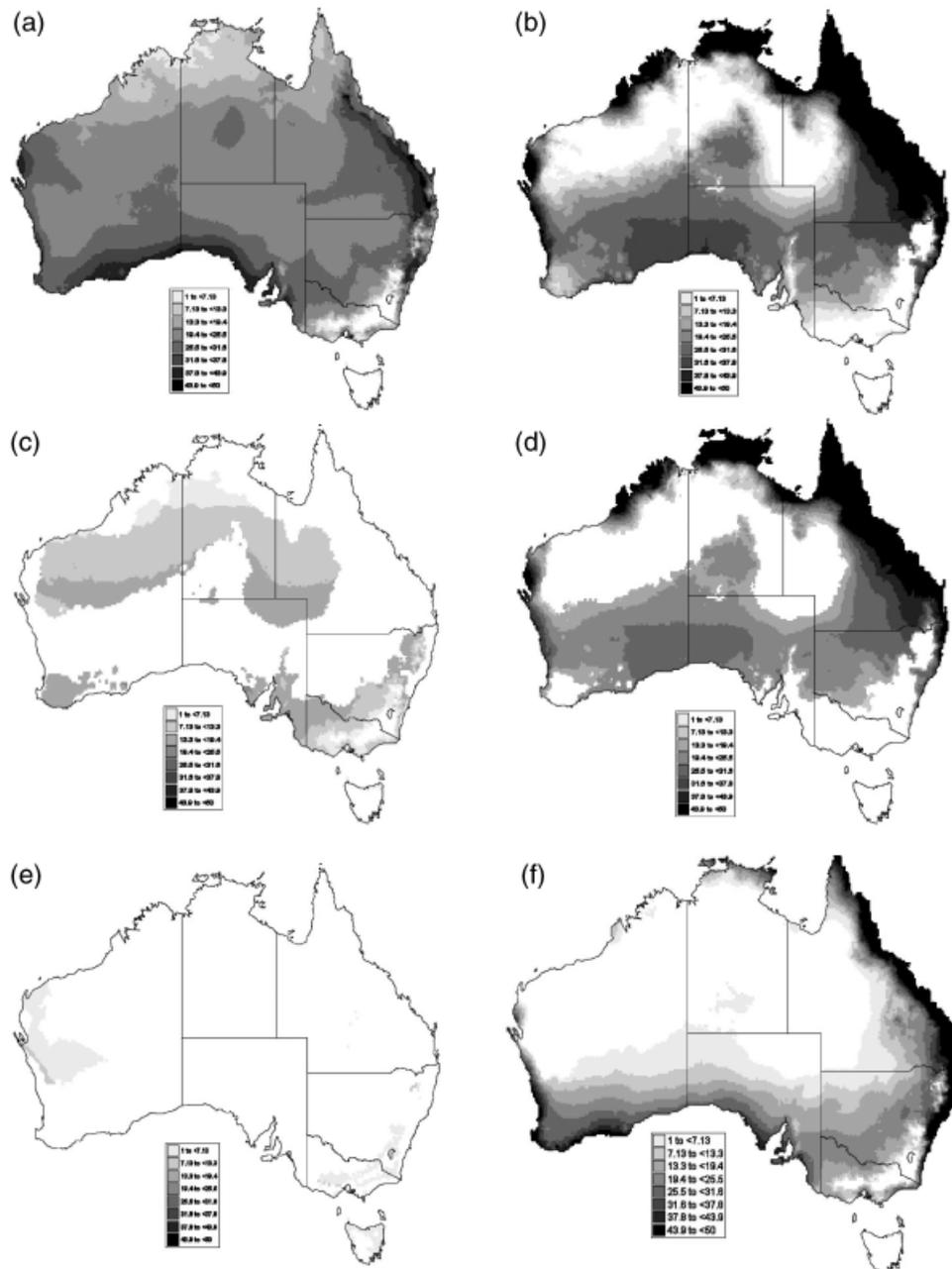


Fig. 6 Potential geographical distributions (CLIMEX™ EI) of the fruit flies (a) *Ceratitis capitata* and (b) *Bactrocera tryoni* in relation to climate in Australia individually; (c) *C. capitata* and (d) *B. tryoni* and when allowed to interact with competitive displacement by the species with the highest annual relative abundance (EI); (e) *C. capitata* and (f) *B. tryoni* with a 2°C climate change scenario and competitive displacement.

interactions are not barriers to projecting the outcomes on geographical scales. There are a number of obvious improvements and caveats to be considered.

The treatment of climatic effects in the CLIMEX™ model has scope for considerable improvement. We need to take account of different regional variances when comparing species responses. We also need to provide a better bridge between use of long-term average data

and data from individual years in order to address effects of climatic variability and extremes on species' geographical distributions. In the current simulations of fruit flies, for example, it is likely that the potential ranges of both species would fluctuate greatly with annual rainfall. Global warming is expected to increase the frequency and intensity of extreme climatic events (Wigley, 1985; IPCC, 2001). Many impacts are likely to

result from such changes and some recent events have been reported (Karl *et al.*, 1996; Nicholls, 2004). Extreme climatic events can be brief and have local impacts (Palmer *et al.*, 2004) or prolonged and have continental scale impacts (Hawkins & Holyoak, 1998) on insect populations. Data on such biological effects need to be interpreted using analytical methods such as those already used in ecology (Gaines & Denny, 1993).

Parameterization of first-order responses in a simple, mechanistic model like CLIMEX™ is relatively straightforward and robust for single species. Nevertheless, the model simulates biological processes and different hypotheses need to be tested when explaining the limits of geographical distributions. Unfortunately, there is a dearth of field observations on changes in population growth and survival rates towards the edges of geographical distributions (Gaston, 1990; Brown *et al.*, 1996). We need to know more about the dynamics of populations along environmental gradients and adjacent to the edges of their ranges (Brown *et al.*, 1996; Sutherst, 2004).

Inclusion of radiation in CLIMEX™ introduces the need to separate the effects of ambient temperature and radiant heat. Plant growth models usually assume that temperature drives development rates while solar radiation drives growth (Monteith, 1977). This appears to ignore radiant heating (Bryant *et al.*, 2002) and its associated microclimatic effects on temperature and evaporation with slope and aspect at a landscape scale and shading at a plant scale. These important effects need to be taken into account with a microclimatic module. This will help to bridge the gap between regional and local relevance of species mapping models, but the global data also need to incorporate the regional effects of 'global dimming' cause by atmospheric pollution (Ramanathan & Ramana, 2005).

Parameterization becomes more complex when the second-order effect of other species on that response is considered. Accumulation of plant growth during the season in CLIMEX™, rather than use of weekly growth rates will provide a better measure of seasonal competitive pressures between species. This will reflect the effects of increasing plant biomass, and hence potential shading or root competition, during the season. In the case of interactions involving three or more species, whether in the same or different trophic levels, parameterization emerges as a significant issue because the number of linkages increases exponentially with the number of species.

Synergy between species raises the issue of the scaling of the growth responses to climate. When conducting experiments on growth responses of species to climate, other variables are usually kept either constant or 'optimal' to reduce variation. For example, historical

experimentation omitted atmospheric CO₂, so the results may underestimate plant growth under current concentrations. In a climatic-response model, such as CLIMEX™, the growth response is scaled between zero and unity. If the response of a single species is less than that of the same species in the presence of a synergistic species, the 'optimal' growth response needs to be redefined and rescaled so as not to exceed unity. We are reviewing the growth parameter values for some species couplets in the light of this requirement. The implications go beyond this local effect to throwing into doubt past descriptions of fundamental niches (Bruno *et al.*, 2003).

Often, and perhaps usually, the geographical distribution of predators is smaller than that of their arthropod (Goolsby *et al.*, 2004), plant (Lawton, 2000; Day *et al.*, 2003) and mammalian (Cumming, 1999) hosts. This suggests that species in higher trophic levels will be more sensitive to climate, as found in a grassland community (Voigt *et al.*, 2003). Caution is needed when using indicators of climatic impacts on predators because results can vary depending on the stage in life-cycle. For example, dryness adversely affects free-living stages of the livestock tick, *B. microplus*, so the direct relationship with climate suggests lower population densities with lower rainfall (Sutherst & Maywald, 1985). When the numbers of maturing parasitic stages are considered, the adverse effects of the same climatic conditions on the host's resistance to tick feeding can increase the proportion of surviving ticks by an order of magnitude (Sutherst *et al.*, 1983). The geographical scale impacts of this effect were investigated by modelling the effect of drought stress on the resistance of cattle to the ticks in the CLIMEX™ model (Sutherst, 1987b). It is now possible to combine the impacts of climate on coupled host-parasite systems.

Our findings on modelling species interactions with CLIMEX™ can be summarized as follows:

1. Early experience has revealed the need to adopt an incremental approach to species analyses in order to define the effects of each environmental variable. We also need to build libraries of relationships for species-couplets (or triplets, etc. but extra species lead to an exponential increase in the parameterization effort) to define their responses to each other and the environment.
2. Truncated geographical distributions can sometimes be used to detect species interactions.
3. Species interactions along environmental gradients can be modelled for those species with derivable CLIMEX™ parameters and can then be projected to other regions. Parameter values can be derived from a combination of field observations and comparative experimental studies of species attributes.

4. Differences in growth potential and direct effects of competitors combine to determine outcomes of competition at each location.
5. The outcomes of the interaction can be sensitive to the parameter values for each species and to annual variation in climate because small differences in the absolute size of the inferred population (*EI*) of a species will allow it to displace the other if there is damaging competition. Accuracy of parameterization is important but difficult to achieve and will need to avoid differences in scaling of the *GIs* for each species. The physics maxim that '*understanding second-order effects requires a higher precision than that for first-order effects*' applies. Sensitivity analysis is essential to determine the potential errors associated with parameter estimation.
6. Where data are not available to parameterize a model CLIMEX™ can answer the question: What does it take, in terms of relative efficiency of use of resources, background predation, host resistance, or greater direct negative effects of a competitor, for one species to displace another from a given location or region?
7. When dispersal rates are low, as in many plants or ant species, a mosaic of species patches is a more likely outcome (Holway *et al.*, 2002; Warren & Topping, 2004). In such cases the CLIMEX™ *EI* values for each species alone provide the best guide to the potential regional distribution, while use of the *Competitive Exclusion* parameter indicates the likely local and ultimate geographical outcomes.
8. *De novo* prediction of the outcomes of invasions with exotic species will remain out of reach for many species, primarily because it is so difficult to identify vacant niches in ecosystems or to define subtle competitive advantages of endemic and exotic species. Opportunities for generalization await a sufficient number of worked examples.
9. Use of network or food web analyses (Memmott *et al.*, 1994; Proulx *et al.*, 2005) may prove to be a more tractable method for investigating the effects of interactions involving multiple species, but their application on large spatial scales has yet to be demonstrated.

Conclusions

With large, nonlinear changes likely to occur in the climate (Calvin, 1998; Curry *et al.*, 2003), and outcomes of many species interactions that are not predictable *a priori* in new ecosystems (Williamson, 1996), the scientific community will never be able to provide definitive answers to questions about risks involving species or communities. The ideal adaptation strategy is to under-

stand a system sufficiently well that designed strategies can be evaluated beforehand and readied for implementation as need arises. Given the multiple uncertainties with global change, other approaches are necessary. Stakeholders need to remain 'nimble' and prepare to respond rapidly to surprises, as they are forced to do under the current biosecurity arrangements. That will be strengthened by a knowledge-based decision-making process (Thomas, 1999), an adaptive management approach (Röling & Wagemakers, 2000) and greater reliance on robust biological solutions (Sutherst *et al.*, 1998). Therein lies a conundrum, because the very methods that we need most may not be fully attainable and we will have to live with uncertainty. We need to acknowledge these omissions and uncertainties. The aims of modelling must be tempered and aimed at reducing the extent of that uncertainty. Decision support systems, designed for sustainability and incorporating sensitivity analyses, are the most promising methods to develop (Sutherst, 2004). These systems need to be embedded within the current pragmatic IPPC approach of reviewing the evidence and relying on expert opinion to identify the ecological factors that may influence a species' distribution, as part of a process of risk analysis (Baker *et al.*, 2000).

Based on our recent experience, and building on the experience of the global change community, we conclude that progress can be made in understanding and extrapolating species interactions along environmental gradients. Global change risk assessments will continue to give 'incorrect' answers no matter how complex they become. We must accept that all laboratory and model results are 'wrong' to various degrees, simply because they are always too simplified to simulate natural systems accurately. The skill is in capturing the major responses that are relevant to the scale of the decision that needs to be made. Lack of precision in projecting potential geographical distributions is not as important as ensuring that the models avoid large and unmeasurable systemic errors (Sutherst & Maywald, 2005). Emphasis needs to be placed on the scientific method and mechanistic approaches, which have much better prospects for further development and contribution to greater understanding. This needs to be coupled with a drive to develop the capacity to generalize species' responses to climate change based on their current ranges. The approach contrasts with the practice of 'stamp collecting' involving the uncritical use of descriptive models on large numbers of species. We need to assess the performance of different analytical approaches that attempt to project species risks under climate change scenarios and for invasive species. This will need truly independent observations (historical time series and species translocations) with blind tests for validation.

Acknowledgements

The Australian Weeds CRC contributed funding to include species interactions into CLIMEX™. Dr Rick Bottomley assisted with the illustrations and citations. Saul Cunningham provided helpful feedback on a draft and Shaun Kolomeitz adapted the high-resolution Australian climatic grid for use in CLIMEX™. Thanks to Drs Dane Panetta, Graeme Hastwell and anonymous referees for helpful advice.

References

- Andrewartha HG, Birch LC (1954) *The Distribution and Abundance of Animals*. University of Chicago Press, Chicago.
- Anonymous (2002) *Predicting Invasions of Nonindigenous Plants and Plant Pests*. National Academy Press, Washington.
- Austin MP (1987) Models for the analysis of species' response to environmental gradients. *Vegetatio*, **69**, 35–45.
- Austin MP, Meyers JA (1996) Current approaches to modelling the environment niche of eucalypts: implication for management of forest biodiversity. *Forest Ecology and Management*, **85**, 95–106.
- Austin MP, Nicholls AO, Doherty MD, Meyers JA (1994) Determining species response functions to an environmental gradient by means of a B-function. *Journal of Vegetation Science*, **5**, 215–228.
- Baker RHA, Sansford CE, Jarvis CH, Cannon RJC, MacLeod A, Walters KFA (2000) The role of climatic mapping in predicting the potential geographical distribution of non-indigenous pests under current and future climates. *Agriculture Ecosystems and Environment*, **82**, 57–71.
- Barton NH, Hewitt GM (1989) Adaptation, speciation and hybrid zones. *Nature*, **341**, 497–503.
- Bosch van der R, Messenger PS (1973) *Biological Control*. Intext Press, New York.
- Bourne AS, Sutherst RW, Sutherland ID, Maywald GF, Stegeman DA (1988) Ecology of the cattle tick (*Boophilus microplus*) in subtropical Australia. III. Modelling populations on different breeds of cattle. *Australian Journal of Agricultural Research*, **39**, 309–318.
- Brown JH, Stevens GC, Kaufman DM (1996) The geographic range: size, shape, boundaries, and internal structure. *Annual Review of Ecology and Systematics*, **27**, 597–623.
- Bruno JF, Stachowicz JJ, Bertness MD (2003) Inclusion of facilitation into ecological theory. *Trends in Ecology and Evolution*, **18**, 119–125.
- Bryant SR, Thomas CD, Bale JS (2002) The influence of thermal ecology on the distribution of three Nymphalid butterflies. *Journal of Applied Ecology*, **39**, 43–55.
- Busby JR (1991) BIOCLIM – a bioclimate analysis and prediction system. *Plant Protection Quarterly*, **6**, 8–9.
- Calvin WH (1998) The great climate flip-flop. *The Atlantic Monthly*, **281**, 47–64.
- Carpenter G, Gillison AN, Winter J (1993) DOMAIN: a flexible modelling procedure for mapping potential distributions of plants and animals. *Biodiversity and Conservation*, **2**, 667–680.
- Chakraborty S, Datta S (2003) How will plant pathogens adapt to host plant resistance at elevated CO₂ under a changing climate. *New Phytologist*, **159**, 733–742.
- Christenson LD, Foote RH (1960) The biology of fruit flies. *Annual Review of Entomology*, **5**, 171–192.
- Coviella CE, Trumble JT (1999) Effects of elevated atmospheric carbon dioxide on insect–plant interactions. *Conservation Biology*, **13**, 700–712.
- Cumming GS (1999) Host distributions do not limit the species ranges of most African ticks (Acari: Ixodida [Metastigmata]). *Bulletin of Entomological Research*, **89**, 303–327.
- Cumming GS (2000) Using habitat models to map diversity: pan-African species richness of ticks (Acari: Ixodida). *Journal of Biogeography*, **27**, 425–440.
- Curry R, Dickson RR, Yashayaev I (2003) A change in the freshwater balance of the Atlantic Ocean over the past four decades. *Nature*, **426**, 826–829.
- Dallwitz MJ, Higgins JP (1978) *User's guide to Devar: A computer program for estimating development rate as a function of temperature*. CSIRO Division of Entomology Report No. 2. 1978. CSIRO Canberra.
- Damman H (1993) Patterns of interaction among herbivore species. In: *Caterpillars. Ecological and Evolutionary Constraints on Foraging* (eds Stamp NE, Casey TM), pp. 132–169. Chapman & Hall, New York.
- Davis AJ, Jenkinson LS, Lawton JH, Shorrochs B, Wood S (1998) Making mistakes when predicting shifts in species range in response to global warming. *Nature*, **391**, 783–786.
- Davis MA, Peltor M (2001) Experimental support for a resource-based mechanistic model of invasibility. *Ecology Letters*, **4**, 421–428.
- Day MD, Broughton S, Hannan-Jones MA (2003) Current distribution and status of *Lantana camara* and its biological control agents in Australia, with recommendations for further biocontrol introductions into other countries. *Biocontrol*, **24**, 63N–76N.
- Duyck P, David P, Quilici S (2004) A review of relationships between interspecific competition and invasions in fruit flies (Diptera: Tephritidae). *Ecological Entomology*, **29**, 511–520.
- Elton CS (1958) *The Ecology of Biological Invasions by Plants and Animals*. Methuen, London.
- FAO (1996) *Guidelines for Pest Risk Analysis. International Standards for Phytosanitary Measures. No. 2*. Food and Agriculture Organisation of the United Nations, Rome.
- Farquhar GD (1997) Carbon dioxide and vegetation. *Science*, **2278**, 1411.
- Gaines SD, Denny MW (1993) The largest, smallest, highest, lowest, longest, and shortest: extremes in ecology. *Ecology*, **74**, 1677–1692.
- Gaston KJ (1990) Patterns in the geographical ranges of species. *Biological Reviews*, **65**, 105–129.
- Goodwin B, McAllister A, Fahrig L (1999) Predicting invasiveness of plant species based on biological information. *Conservation Biology*, **13**, 422–426.
- Goolsby JA, De Barro PJ, Kirk AA *et al.* (2004) Post-release evaluation of the biological control of *Bemisia tabaci* biotype 'B' in the USA and the development of predictive tools to guide introductions for other countries. *Biological Control*, **32**, 70–77.
- Guisan A, Zimmermann NE (2000) Predictive habitat distribution models in ecology. *Ecological Modelling*, **135**, 147–186.
- Harrington R, Woiwod I, Sparks T (1999) Climate change and trophic interactions. *Trends in Ecology and Evolution*, **14**, 146–150.

- Hawkins BA, Holyoak M (1998) Transcontinental crashes of insect populations? *American Naturalist*, **152**, 480–484.
- Hill JK, Collingham YC, Thomas CD, Blakeley DS, Fox R, Moss D, Huntley B (2001) Impacts of landscape structure on butterfly range expansion. *Ecology Letters*, **4**, 313–321.
- Holway DA, Suarez AV, Case TJ (2002) Role of abiotic factors in governing susceptibility to invasion: a test with argentine ants. *Ecology*, **83**, 1610–1619.
- Howell CJ, Walker JB, Nevill EM (1978) *Ticks, mites and insects infesting domestic animals in South Africa. Part 1. Descriptions and biology*. Science Bulletin 1–69. 1978. Onderstepoort, Department of Agricultural Technical Services Republic of South Africa.
- Hulme PE (2003) Biological invasions: winning the science battles but losing the conservation war? *Oryx*, **37**, 178–193.
- Huxel GR (1999) Rapid displacement of native species by invasive species: effects of hybridization. *Biological Conservation*, **89**, 143–152.
- IPCC (2001) *Climate Change 2001 Third Assessment Report*. Cambridge University Press, Cambridge.
- Jones T, Thompson L, Lawton J *et al.* (1998) Impacts of rising atmospheric carbon dioxide on model terrestrial ecosystems. *Science*, **280**, 441–443.
- Karl TR, Knight RW, Plummer N (1996) Trends in high-frequency climate variability in the twentieth century. *Nature*, **377**, 217–220.
- Keeling CD, Whorf P (2004) Atmospheric CO₂ records from sites in the SIO air-sampling network. In: *Trends Online: A Compendium of Data on Global Change*. Carbon Dioxide Information Analysis Center, Oak Ridge National Laboratory, US Department of Energy, Oak Ridge, USA.
- Keiser I, Kobayashi RM, Miyashita DH, Harris EJ, Schneider EL, Chambers DL (1974) Suppression of Mediterranean fruit flies by oriental fruit flies in mixed infestations in guava. *Journal of Economic Entomology*, **67**, 355–360.
- Kingsolver JG (1979) Thermal and hydric aspects of environmental heterogeneity in pitcher plant mosquito. *Ecological Monographs*, **49**, 357–376.
- Kingsolver JG (1989) Weather and the population dynamics of insects: integrating physiological and population ecology. *Physiological Zoology*, **62**, 314–334.
- Körner C (2000) Biosphere responses to CO₂ enrichment. *Ecological Applications*, **10**, 1590–1619.
- Kriticos DJ, Randall PR (2001) A comparison of systems to analyse potential weed distributions. In: *Weed Risk Assessment* (eds Groves RH, Panetta FD, Virtue JG), pp. 61–79. C.S.I.R.O, Melbourne.
- Lawton JH (2000) *Community Ecology in a Changing World*. Ecology Institute, Oldendorf/Luhe, Germany.
- Lawton JH, Hassell MP (1981) Asymmetrical competition in insects. *Nature*, **289**, 793–795.
- Leemans R (1996) Incorporating land-use change in Earth system models illustrated by IMAGE 2. In: *Global Change and Terrestrial Ecosystems* (eds Walker BH, Steffen W), pp. 484–510. Cambridge University Press, Cambridge.
- MacArthur RH (1972) *Geographical Ecology: Patterns in the Distribution of Species*. Harper & Row, New York.
- Mattson WJ, Haack RA (1987) The role of drought in outbreaks of plant-eating insects. Drought's physiological effects on plants can predict its influence on insect populations. *BioScience*, **37**, 110–118.
- Maywald G, Kriticos D, Sutherst R, Bottomley W (2004a) *DY-MEX V2. Model Builder User's Guide*. Hearne Scientific Software Inc, Melbourne.
- Maywald G, Sutherst R, Bourne A (2004b) *DYMEX V2. Model Simulator User's Guide*. Hearne Scientific Software Inc., Melbourne.
- Memmott J, Godfray HCJ, Gould ID (1994) The structure of a tropical host-parasitoid community. *Journal of Animal Ecology*, **63**, 521–540.
- Mitchell CE, Power AG (2003) Release of invasive plants from fungal and viral pathogens. *Nature*, **421**, 625–627.
- Monteith JL (1977) Climate and efficiency of crop production in Britain. *Philosophical Transactions Royal Society London, B*, **281**, 277–294.
- Mooney HA, Cropper A, Reid W (2004) The millennium ecosystem assessment: what is it all about? *Trends in Ecology and Evolution*, **19**, 221–224.
- Mooney HA, Hobbs RJ (2000) *Invasive Species in a Changing World*. Island Press, Corelo, CA.
- Navas ML (1998) Individualistic species performance and response of multi-specific communities to elevated CO₂: a review. *Functional Ecology*, **12**, 721–727.
- New M, Lister D, Hulme M, Makin I (2002) A high-resolution data set of surface climate over global land areas. *Climate Research*, **21**, 1–25.
- Nicholls N (2004) The changing nature of Australian droughts. *Climatic Change*, **63**, 323–336.
- Nicholson AJ (1958) Dynamics of insect populations. *Annual Review of Entomology*, **3**, 107–136.
- Nikolov NT, Zeller KF (1992) A solar radiation algorithm for ecosystem dynamic models. *Ecological Modelling*, **61**, 149–168.
- Norval RAI, Perry BD (1990) The introduction, spread and subsequent disappearance of the brown ear-tick, *Rhipicephalus appendiculatus* from the southern lowveld of Zimbabwe. *Experimental and Applied Acarology*, **9**, 103–111.
- Norval R, Sutherst R (1986) Assortative mating between *Boophilus decoloratus* and *Boophilus microplus* (Acari: Ixodidae). *Journal of Medical Entomology*, **23**, 459–460.
- Palmer WA, Day MD, Dhileepan K, Snow EL, Mackey AP (2004) *Analysis of the non-target attack by the lantana sap-sucking bug, Aconophora compressa and its implications for biological control in Australia*. Proceedings of the 14th Australian Weeds Conference. 2004.
- Park T (1948) Experimental studies of interspecies competition. I. Competition between populations of flour beetles *Tribolium confusum* and *Tribolium castaneum* Herbst. *Ecological Monographs*, **18**, 265–308.
- Pearson RG, Dawson TP, Berry PM, Harrison PA (2002) SPECIES: a spatial evaluation of climate impact on the envelope of species. *Ecological Modelling*, **154**, 289–300.
- Peel MC, McMahon TA, Finlayson BL (2004) Continental differences in the variability of annual runoff-update and reassessment. *Journal of Hydrology*, **295**, 185–197.

- Peterson AT, Ortega-Huerta MA, Bartley J, Sanchez-Cordero V, Soberon J, Buddemeier RH, Stockwell DRB (2002) Future projections for Mexican faunas under global climate change scenarios. *Nature*, **416**, 626–629.
- Proulx SR, Promislow DEL, Phillips PC (2005) Network thinking in ecology and evolution. *Trends in Ecology and Evolution*, **20**, 345–353.
- Pyke C, Fischer D (2005) Selection of bioclimatically representative biological reserve systems under climate change. *Biological Conservation*, **121**, 429–441.
- Ramanathan V, Ramana M (2005) Persistent, widespread, and strongly absorbing haze over the Himalayan foothills and the Indo-Gangetic plains. *Pure and Applied Geophysics*, **162**, 1609–1626.
- Rogers KJ, Randolph SE (1993) Distribution of tsetse and ticks in Africa: past, present and future. *Parasitology Today*, **9**, 266–271.
- Röling NG, Wagemakers MAE (2000) *Facilitating Sustainable Agriculture: Participatory Learning and Adaptive Management in Times of Environmental Uncertainty*. Cambridge University Press, Cambridge.
- Room PM, Julien MH, Forno IW (1989) Vigorous plants suffer most from herbivores: latitude, nitrogen and biological control of the weed *Salvinia molesta*. *Oikos*, **54**, 92–100.
- Schlesinger WH (1977) *Biogeochemistry – An Analysis of Global Change*. Academic Press, San Diego.
- Siemann E, Rogers WE (2003) Increased competitive ability of an invasive tree may be limited by an invasive beetle. *Ecological Applications*, **13**, 1503–1507.
- Silvertown J (2004) The ghost of competition past in the phylogeny of Island endemic plants. *Journal of Ecology*, **92**, 168–173.
- Southwood TRE (1977) Habitat, the templet for ecological strategies? *Journal of Animal Ecology*, **46**, 337–365.
- Sutherst RW (1987a) The dynamics of hybrid zones between tick (Acari) species. *International Journal for Parasitology*, **17**, 921–926.
- Sutherst RW (1987b) Ectoparasites and herbivore nutrition. In: *The Nutrition of Herbivores. 2nd International Symposium on the Nutrition of Herbivores* (eds Hacker JB, Ternouth JH), pp. 191–209. Academic Press, Sydney.
- Sutherst RW (1998) Implications of global change and climate variability for vector-borne diseases: generic approaches to impact assessments. *International Journal for Parasitology*, **28**, 935–945.
- Sutherst RW (2000) Climate change and invasive species – a conceptual framework. In: *Invasive Species in a Changing World* (eds Mooney HA, Hobbs RJ), pp. 211–240. Island Press, Washington, DC.
- Sutherst RW (2001) The vulnerability of animal and human health to parasites under global change. *International Journal for Parasitology*, **31**, 933–948.
- Sutherst RW (2003) Prediction of species geographical ranges. Guest editorial. *Journal of Biogeography*, **30**, 1–12.
- Sutherst RW (2004) Global change and human vulnerability to vector-borne diseases. *Clinical Microbiology Reviews*, **17**, 136–173.
- Sutherst RW, Floyd RB, Maywald GF (1995) The potential geographical distribution of the cane toad, *Bufo marinus* L. in Australia. *Conservation Biology*, **9**, 294–299.
- Sutherst RW, Ingram J, Scherm H (1998) Global change and vector-borne diseases. *Parasitology Today*, **14**, 297–299.
- Sutherst RW, Kerr JD, Maywald GF, Stegeman DA (1983) The effect of season and nutrition on the resistance of cattle to the tick *Boophilus microplus*. *Australian Journal of Agricultural Research*, **34**, 329–339.
- Sutherst RW, Maywald G (2005) A climate-model of the red imported fire ant, *Solenopsis invicta* Buren (Hymenoptera: Formicidae): implications for invasion of new regions, particularly Oceania. *Environmental Entomology*, **34**, 317–335.
- Sutherst RW, Maywald GF (1985) A computerized system for matching climates in ecology. *Agriculture Ecosystems and Environment*, **13**, 281–300.
- Sutherst RW, Maywald GF, Bourne AS (2004) *CLIMEX Version 2. User's Guide*. Hearne Scientific Software Inc., Melbourne.
- Sutherst RW, Maywald GF, Russell BL (2000) Estimating vulnerability under global change: modular modelling of pests. *Agriculture Ecosystems and Environment*, **82**, 303–319.
- Sutherst RW, Maywald GF, Skarratt DB (1995a) Predicting insect distributions in a changed climate. In: *Insects in a Changing Environment* (eds Harrington R, Stork NE), pp. 59–91. Academic Press, London.
- Sutherst RW, Maywald GF, Skarratt DB (1995b) Predicting insect distributions in a changing climate. In: *Insects in a Changing Environment* (eds Harrington R, Stork NE), pp. 59–91. Academic Press, London.
- Sykes MT, Prentice IC (2004) Boreal forest futures. Modelling the controls on tree species range limits and transient responses to climate change. *Water, Air, and Soil Pollution*, **82**, 415–428.
- Thomas D, Cameron A, Green RE *et al.* (2004) Extinction risk from climate change. *Letters to Nature*, **427**, 145–148.
- Thomas MB (1999) Ecological approaches and the development of 'truly integrated' pest management. *Proceedings of the National Academy of Sciences*, **96**, 5944–5951.
- Thuiller W (2003) Biomod – optimizing predictions of species distributions and projecting potential future shifts under global change. *Global Change Biology*, **9**, 1353–1362.
- Torchin ME, Lafferty KD, Dobson AP, McKenzie VJ, Kuris AM (2003) Introduced species and their missing parasites. *Nature*, **421**, 628–630.
- Utech KBW, Wharton RH, Kerr JD (1978) Resistance to *Boophilus microplus* (Canestrini) in different breeds of cattle. *Australian Journal of Agricultural Research*, **29**, 885–895.
- Vera MT, Rodriguez R, Segura DF, Cladera JL, Sutherst RW (2002) Potential geographical distribution of the Mediterranean fruit fly, *Ceratitidis capitata* (Diptera: Tephritidae), with emphasis on Argentina and Australia. *Environmental Entomology*, **31**, 1009–1022.
- Vitousek PM, Aber JD, Howarth RW *et al.* (1997) Human alteration of the global nitrogen cycle: sources and consequences. *Ecological Applications*, **7**, 737–750.
- Voigt W, Perner J, Davis AJ *et al.* (2003) Trophic levels are differentially sensitive to climate. *Ecology*, **84**, 2444–2453.
- Walker B, Steffen W, Canadell J, Ingram J (1999) *The Terrestrial Biosphere and Global Change*. Cambridge University Press, Cambridge.
- Walker BH, Steffen WL (1999) The nature of global change. In: *The Terrestrial Biosphere and Global Change. Implications for Natural and Managed Ecosystems* (eds Walker B, Steffen W,

- Canadell J, Ingram J), pp. 1–18. Cambridge University Press, Cambridge, UK.
- Walker PA, Cocks KD (1991) HABITAT: a procedure for modelling a disjoint environmental envelope for a plant or animal species. *Global Ecology and Biogeography letters*, **1**, 108–118.
- Warren J, Topping C (2004) A trait specific model of competition in a spatially structured plant community. *Ecological Modelling*, **180**, 477–485.
- Wedderburn PA, Jagger TD, McCartan B, Hunter AG (1991) Distribution of *Boophilus* species ticks in Swaziland. *Tropical Animal Health and Production*, **23**, 167–171.
- White N, Sutherst RW, Hall N, Whish-Wilson P (2003) The vulnerability of the Australian beef industry to impacts of the cattle tick (*Boophilus microplus*) under climate change. *Climate Change*, **61**, 157–190.
- Wigley TML (1985) Impact of extreme events. *Nature*, **316**, 106–107.
- Williamson M (1996) Which communities are invaded by which type of species? In: *Biological Invasions* (ed. Williamson M), pp. 55–79. Chapman & Hall, London.
- Williamson MH, Fitter A (1996) the characters of successful invaders. *Biological Conservation*, **78**, 163–170.
- Yonow T, Sutherst RW (1998) The geographical distribution of the Queensland fruit fly, *Bactrocera (Dacus) tryoni*, in relation to climate. *Australian Journal of Agricultural Research*, **49**, 935–953.