

Prediction of species geographical ranges

A critical comment on M. J. Samways, R. Osborn, H. Hastings & V. Hattings (1999) Global climate change and accuracy of prediction of species geographical ranges: establishment success of introduced ladybirds (Coccinellidae, *Chilocorus* spp.) worldwide. *Journal of Biogeography*, 26, 795–812.

GUEST EDITORIAL

The use of climate matching to improve the success rate of introductions of biological control agents into new environments is well-established (DeBach, 1964). Similarly, there have been robust examples where the risk of establishment of invasive species has been successfully defined *a priori* using climatic modelling. These include: *Leptinotarsa decemlineata* (Say) in Europe (Sutherst *et al.*, 1991), *Amblyomma variegatum* (Fabricius) and *A. hebraeum* (Koch) in Zimbabwe (Bruce & Wilson, 1998); *Chrysomya bezziana* (Villeneuve) in Ethiopia (Hall & Wall, 1995) and *Boophilus microplus* (Canestrini) in east and southern Africa (Sutherst, 2001).

Samways *et al.* (1999) claim to have tested ‘how accurate predictions of range change might be before entertaining global climatic change’. They attempted to do this by using climate matching to predict the success of establishment of fifteen species of ladybirds (Coccinellidae, *Chilocorus* spp.), which had been the subject of efforts to spread them beyond their native ranges to enhance biological control. The ‘percent correct predictions of establishment’ was the criterion used to test their hypothesis, expressed also as ‘predicting species climatic tolerances’. After achieving an apparently low success rate, they concluded 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’. I discuss here how such a statement demonstrates weak scientific inference.

Samways *et al.* used the CLIMEX model (Sutherst & Maywald, 1985; Sutherst *et al.*, 1995, 1999) and its associated ‘Match Climates’, climate-matching algorithm to make their predictions. The CLIMEX model is a simulation model of moderate complexity for inferring the responses of a species to climate from its geographical distribution. Once response functions have been fitted, the model can be run with meteorological data from other parts of the world to estimate the species response to new climatic environments. The *potential* range, as determined by climate, can then be estimated. The model parameter values constitute the hypotheses on the climatic factors that determine the species population growth, and survival during adverse seasonal conditions, and so limit the geographical distribution. Alternatively, the meteorological data base can be manipulated to create scenarios of climate change.

Samways *et al.* attempted to explain the success or otherwise of particular introductions of *Chilocorus* species to new environments based on their estimated potential climatic range. This assumes that both the claims of the predictive success of climate matching, in this case using CLIMEX, and the base rates for establishment of exotic introductions are both 100%. However, Smith *et al.* (1999) showed that low base rates for establishment of exotic species influence the reliability of predictive tools. In the field of biological control, using arthropods, the base rates are in fact quite high, at around 65% (Julien *et al.*, 1984; Waterhouse & Sands, 2001). Nevertheless such a suboptimal base rate caps the maximum success rate for predictions below the accuracy that is estimated on the assumption that all introductions into suitable climates will be successful.

Sutherst & Maywald (1985) stated a caveat that users of CLIMEX need to exclude non-climatic factors limiting the distribution before assuming that climate is the only factor. The CLIMEX model, or other climate-matching tools, do not pretend to predict the outcome of particular introduction events. They define the role of climate as a factor in determining the potential for establishment when all other factors are not included. In addition, the CLIMEX software includes a facility for comparing meteorological data from different places (Match Climates). Samways *et al.* also used this algorithm in their efforts to explain the outcomes of introductions.

A comprehensive response to correct errors in Samways *et al.* would have required many weeks of literature reviews and re-calculations of their analysis of each species, which was not practical. Rather, I point out examples of the main types of factual and methodological errors, inappropriate assumptions and omissions in the paper and show why the results of their analyses are invalid and their conclusions are not logical. I then investigate re-fitting of the parameter values of the CLIMEX model for one species – *C. cacti* (Linnaeus 1767) – to illustrate how the modelling is recommended to be carried out.

OUTLINE OF CLIMEX SOFTWARE AND MODEL

Before proceeding further, we need to distinguish between the CLIMEX model and the CLIMEX software package. The software contains two distinct functions: first, a species-specific response model (CLIMEX), which can be run in either 'Compare Locations' or 'Compare Years' modes. For present purposes we need only to be concerned with the former mode in which the suitability of different geographical locations for a given species is compared, based on long-term average meteorological data. Secondly, the software contains an algorithm, 'Match Climates', for simply comparing meteorological data at different locations.

The CLIMEX model

A brief outline of the CLIMEX model is necessary to explain the deficiencies in the Samways *et al.* paper. Sutherst & Maywald (1985) gave the original description of the model. Since then many other features, insights and caveats have been described by Maywald & Sutherst (1991), Sutherst *et al.* (1995, 1996, 1999, 2000), Sutherst (1998, 2000a, 2001) and Yonow & Sutherst (1998). The software has been used extensively in the fields of biological control, climate change and pest risk assessment with positive results in many countries. A list of *c.* 150 citations is provided at: <http://www.ento.csiro.au/climex/climex.html>. Samways *et al.* seem to be unaware of the considerable CLIMEX literature.

The CLIMEX model is designed to extract maximum information on the response of a species to climate out of minimal field data. It derives weekly and annual indices that describe the responses of a nominated species to temperature and moisture, and light in the case of plants. The model is based on a conceptual model that there are two types of seasons each year – one with population growth and the other with population decline (Fig. 1). These are referred to as *growth* and *survival* or *stress* seasons, respectively. A population has to be able to survive during the stressful season, with its negative effects on population density, in order to exist at the start of the favourable season (unless it is a migratory species). In practice there are exceptions to this rule in small regions of the world, such as East Africa where there are two stressful (dry) seasons. They need additional interpretation of CLIMEX seasonal results. The overall climatic suitability of a nominated location for a given organism is provided by an 'Ecoclimatic Index' (EI, scaled from 0 to 100), which combines the annual potential for population growth with the annual stress. As the EI is an aggregate measure, it alone is inadequate to explain an organism's response to climate. The model parameter values for growth and stress constitute the description of the organism's response to climate and, as such, they represent the hypotheses to be tested. Testing demands that, like any mathematical model, the parameter values are published so that the results can be repeated and the values challenged and refined as further observations become available.

CLIMEX incorporates a hydrological model to integrate the effects of rainfall and evaporation into a 'moisture index', which describes the availability of soil moisture to plants or animals. The index is then combined with a temperature response curve to produce weekly and annual 'Growth Indices' (GI_W and GI_A , respectively, with the former scaled between 0 and 1 and the latter between 0 and 100). Any suboptimal weekly values of either temperature or moisture reduce the values of the growth index from its potential. This point is particularly pertinent to the current critique.

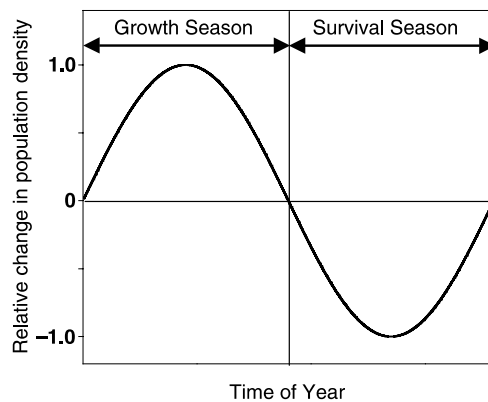


Figure 1 Schematic diagram showing the year conceptually divided into two seasons, one for population growth and one for survival of stressful climatic conditions, when using the CLIMEX model.

Extreme values and duration of temperature and moisture limit the survival of populations, and so set the ultimate bounds of the potential geographical range as determined by climate. In CLIMEX, their effects are described by four annual 'Stress Indices': wet, dry, cold and hot, that estimate the threat to that species posed by prolonged or intensely extreme periods of adverse conditions, and their interactions where appropriate. The weekly values of each stress index are accumulated using a nonlinear function to give an annual value. If that value exceeds 100, the species is deemed not to be able to persist in that environment.

The EI gives an overall measure of the suitability of a given location for permanent occupation by a species. It is therefore a measure that is both species-specific and location-specific, and implies that establishment is only possible when the value exceeds zero. In practice, with variable seasons, values of $EI < 10$ indicate that the location is marginal for the species and large annual fluctuations in numbers are likely. A location can only have a perfect suitability for a species ($EI = 100$) if it provides ideal conditions throughout the year for that species. We saw above how the year can be divided into favourable and stressful seasons. One consequence of this assumption is that in temperate regions or other regions with distinct wet and dry seasons, the *maximum* achievable value of the EI is likely to be around 50. In practice, values in excess of 20 have been found to support substantial population densities and values in excess of 50 are rare and usually confined to the wet tropics.

CLIMEX analyses usually require that a species climatic requirements are inferred from information on its known geographical distribution, relative abundance and seasonal phenology. This 'top-down' procedure is called 'inverse' or 'inferential' modelling and it is the reverse of the reductionist approach usually used to build mechanistic models. Where laboratory data are available, they can be used to bolster the model fitting process or to explain the processes. The aim is to capture the core features of the species climatic requirements from minimal observations, not to describe the population dynamics in detail. CLIMEX analyses have proved very illuminating even with species that have been studied intensively. This is partly because CLIMEX starts with the geographical distribution, which is the result of the integration of the influences of all the factors affecting the life cycle. The model is designed to mimic the integration of all the climatic influences on populations at each location. Given the huge range of possible, seasonal permutations of temperature and moisture associated with locations spread across geographical space (Sutherst, 1998), the fitting process is, in fact, very demanding of the model. In order to function on a global scale, the parameter values of a CLIMEX model for a given species need to be valid over a very wide range of values of temperature and moisture. These demands partly explain why the results can be quite robust. In contrast, with a reductionist approach, it is difficult to define limiting climatic factors over a useful range of parameter values. Thus both reductionist and inferential modelling approaches have strengths and weaknesses, and they complement each other in ecological investigations. Indeed, I never start a fresh ecological study (or overseas travel) without doing a CLIMEX analysis first, because it provides such a useful geographical and climatic context, within which site-specific observations can be more readily interpreted (Sutherst, 2001).

Two of Sutherst & Maywald's (1985) caveats on the CLIMEX model in relation to the process of inferring climatic responses from geographical distributions are pertinent to the current discussion. The first is that the process can only define climatic limits if the original distribution covers a sufficiently large and/or heterogeneous area. This is needed to provide the necessary range of possible temperature and moisture values for fitting parameters. If the original distribution is very much restricted, perhaps through historical lack of opportunities to migrate for example, or does not cover a sufficiently heterogeneous area, there is little alternative but to leave some limits undefined or to estimate them from other information. For example, Mediterranean climates do not expose species to hot-wet conditions, so the ability of species from those areas to survive such conditions in summer rainfall areas is not definable *a priori*, but it can be assumed – as a working hypothesis – that they will be poorly adapted to them. Where irrigation is practiced in such environments, it can provide some insights into the likely response of the species to summer rainfall.

The second caveat relates to any assumption that climate alone limits the geographical distribution. Naturally, that is not the case because biological or other physical factors reduce the population growth and so may prevent the species from occupying the whole area that is climatically suitable for it, referred to as the fundamental niche (Hutchinson, 1957/8). Sutherst & Maywald (1985) gave an example of how most of sub-Saharan Africa is climatically suitable for the Asian livestock tick (*Boophilus microplus*), but its ability to invade the region has been impeded by unstable interspecific interactions with the local species, *B. decoloratus* (Koch) (Sutherst, 1987) and low movement rates. Since that time *B. microplus* has invaded large areas in southern Africa and Tanzania, as movement

restrictions on cattle have been relaxed, allowing an increase in the propagule pressure that is needed to overcome the barrier provided by *B. decoloratus* (Sutherst, 2001).

Gutierrez (2000) described the seasonal growth index of Fitzpatrick & Nix (1970), which was adapted by Sutherst & Maywald (1985) and incorporated into the CLIMEX model. He also discussed the physiological basis of the growth index concept, and applications of a tri-trophic (plant/herbivore/predator) growth index approach to impact assessments under climate change. However, there is scope for confusion with the CLIMEX model because the model described by Gutierrez was confined to the description of population growth during the favourable season, not to survival during the adverse season. The absence of growth was taken as an inability to survive without any description of the mechanism or cause of mortality involved. This differs fundamentally from the core CLIMEX 'stress' functions for estimating limiting factors when predicting geographical distributions. These stress functions attempt to mimic the biological processes that limit species in extreme climatic conditions. Instead Gutierrez used modified climograms (Cook, 1925) based on seasonal patterns of growth indices in different habitats to delimit the climatic range of a species.

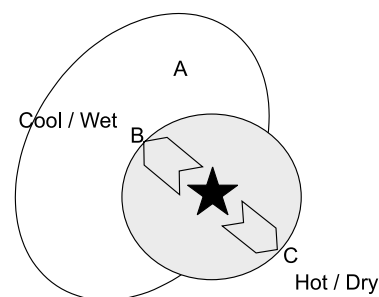
A second major difference is that Fitzpatrick & Nix (1970) and Gutierrez (2000) approached the use of growth indices using a physiological, reductionist approach. In contrast, the real power of the CLIMEX model, in the present context, is the application of an inverse or inferential modelling approach. The 'data' is the geographical distribution and any field observations on relative abundance in different seasons. The model fitting process works in reverse to infer what climatic processes determine that distribution. This is necessary when appropriate experimental data are not available, which is usually the case for all but the most intensively studied species. CLIMEX is based on 'the art of the possible', referred to by Worner (1991) as a pragmatic approach. I urge users to 'listen to CLIMEX' when fitting model parameters, rather than force parameter values from laboratory studies into the model. Once the iterative process has provided one or more adequate descriptions or explanations of the geographical distribution of the species, the parameter values are examined for insights into the species responses to climate. These can form the basis for more informed experimental research. Forcing a physiological approach onto the model fitting process is a two-edged sword, in that it can strengthen the description of some processes, but it is at the risk of over-riding some epidemiological processes that are occurring in the field. Consistency between the results from using both approaches increases confidence in the interpretation of the physiological processes limiting a species geographical distribution.

Match Climates

The second function in the CLIMEX software package is 'Match Climates'. This function is designed simply to compare meteorological data from different locations. That is often the only option available, for example when targeting collection sites for searches of new, as yet unidentified biological control agents that will be adapted to the climate at the proposed destination. We refer to the Match Climates function as the *poor man's* option, because it addresses the situation where no knowledge is available on the distribution of the species and it therefore provides much less intelligent information than the CLIMEX model. The function generates a climate *Match Index*, MI (unfortunately with the same acronym as the Moisture Index in the CLIMEX simulation model above and since changed to CMI). The index is analogous to a correlation coefficient but it is scaled to make it more sensitive to small deviations in the range of interest, i.e. 0.6–1.0. Based on past experience, values of MI < 0.60 indicate poor matches between locations, with the potential for significantly different limiting effects of some variables in some of the locations. Hence, as a rule-of-thumb only, similarities of this order or less are not considered to be promising in terms of finding well-adapted species to introduce into the matching location. A number of caveats are necessary when using the function. Sutherst *et al.* (2000) emphasized the need to support the index with visual assessment of the data to see whether deviations between locations were positive or negative. Deviations from a given location in the direction of a species range boundary will give opposite conclusions to deviations in the direction of the core of the species climatic envelope, as illustrated schematically in Fig. 2. While the climates at the extremities of the circle at points B and C have the same similarity (Match Index) to the location marked with a star, B is more favourable for the species while C is unfavourable. Thus there is an asymmetry in the index when compared with the geographical distribution A, which is indefinable under these circumstances where the geographical distribution is unknown.

In addition, a climate that has a smaller annual range of temperature and moisture parameters, and thus is potentially more suitable, may have a poor match when compared with the climate of areas

Figure 2 Schematic illustration of the overlap between the range of a CLIMEX Match Climates index (shaded circle) and a hypothetical geographical distribution of a species in the unshaded oval, A. Point 'B' lies inside the distribution of the species while point 'C' lies outside it, despite both locations having the same CLIMEX Match Index.



where the species occurs (Csurhes & Kriticos, 1994). For example, it is possible to have a very low value of MI when comparing tropical highland locations with temperate regions, because the former climate may represent year-round ideal summer conditions for a species that originated in the temperate zone (Sutherst *et al.*, 1996). One such example is the explosive success of conifer aphids of European origin in the highlands of Kenya (Mills, 1990). A comparison of the meteorological data of the two regions gives a very low MI value because there is no winter in Kenya. Nevertheless, the potential for population growth of a temperate species in the Kenya highlands is similar to a year-round summer in a temperate region with no winter constriction of the population.

These features of climatic comparisons, that are made using Match Climates, affect all other algorithms that are used to compare climates, except the CLIMEX model above and STASH (Sykes *et al.*, 1996), which do not rely on pattern-matching of meteorological data (Kriticos & Randall, 2001). They demand that caution be taken when applying them.

SPECIFIC CRITICISMS OF SAMWAYS ET AL.

Match Climates

Samways *et al.* used the CLIMEX *Match Climates* function to compare the climates of areas-of-origin with areas-of-introduction of the fifteen species of ladybirds. They quoted Sutherst & Maywald (1990) as suggesting that '0.6 is the critical value below which an introduction of a species is unlikely to establish permanently'. No such quote exists in the cited paper. What has been stated elsewhere is that 'Experience suggests that a value of 0.6 is the lowest that is usually useful' (Maywald & Sutherst, 1991). This is an arbitrary value, and it is quite inappropriate to use it uncritically as Samways *et al.* (1999) did to select areas where their introduced species were implied to be able to establish. They chose a threshold value of $MI = 0.6$ to separate locations in which establishment of introductions was implied from those in which the species failed. None of the caveats referred to above were taken into account.

In addition they state: 'The favourableness/suitability of a location for species development and survival were determined using the 'match climates' routine of CLIMEX'. As the Match Climates function does not relate to a species, it appears that they inferred that locations with climatic similarity within the range of 0.6–1.0 would support the species. If the MI is equal to (say) 0.6 it indicates a certain level of similarity but that *per se* does not reveal whether the deviations from the climate of the matched location are more or less suitable for any given species. Hence the need for caution when using values as low as 0.6 to infer similarity of climates for a particular species.

CLIMEX model

CLIMEX modelling aims to determine the *potential* range, on the assumption that all other non-climatic constraints are absent. Thus Samways *et al.*'s use of the 'percent correct predictions of establishment' of particular introductions to test their hypothesis that the range can be determined using climate alone was inappropriate in light of the 'tens' rule (Williamson & Fitter, 1996). With a success rate of *c.* 27% in predicting the outcomes of introductions by climate-matching, albeit with faulty data and a misunderstood model as explained below, they went on to conclude that the range cannot always be determined by climatic-matching and so 'most predictions of range change with climate change are likely to be wrong'. This is not a logical conclusion. The outcome of a particular introduction cannot logically be equated with the species range. The failure of particular introductions of a species to establish in a new area does not necessarily mean that the climate is unsuitable. Conversely, a suitable

climate does not ensure successful establishment. This is why the practice of biological control relies on creating enough propagule pressure to ensure that there is a critical mass of individuals to establish in the face of environmental resistance from such factors as native predators or parasitoids (Robertson 1986; Semple & Forno, 1987) or poor host plant nutritional status (Dodd, 1936; Room & Thomas, 1985).

Quite apart from these logical errors, it is evident from the description of Samways *et al.*'s methods and results that they misunderstood the model and used an inappropriate parameter-fitting process. The consequence is that their analyses are so confused and erroneous that their results and conclusions are meaningless.

It is difficult to follow the process that Samways *et al.* used to estimate the CLIMEX model parameter values from their description of the methods. Within the methods they made a number of apparently contradictory statements. They stated that 'the Ecoclimatic Indices (EI) 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.... 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.... Establishment was implied if the EI and GI were both 75 or above, and MI (from the Match Climates function) was 0.6 or above.... The favourableness/suitability of a location for species development and survival were determined using the 'match climates' routine of CLIMEX, and the EIs were determined for all areas.... The model, however assumes that all species are equally sensitive to the same climatic tolerance... 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 the species geographical ranges fitted well'. These determinations appear to be the main source of the confusion. As far as it is possible to understand from this description of the methods, it appears that the conditions for growth were greatly overestimated. In addition, the limiting effects of extreme climatic conditions, as described by the CLIMEX stress indices, do not appear to have been taken into account when fitting the model to the geographical distribution of each species, although there is one reference to them. As none of the model parameter values for any of the species was included in the paper, their values could not be examined. The combined measures of success using both the EI and GI values are a tautology, as the EI already incorporates the information from the GI. The additional step of including the MI has a degrading effect on the measure of success by diluting what should be 'intelligent', species-specific information with poorer quality, non-specific information.

We saw above how the year can be divided conceptually into favourable and stressful seasons and how it means that the *maximum* achievable value of the EI is likely to be around 50 in most regions of the world with either a cold or dry season. Yet Samways *et al.* quote numerous examples where both the annual GI and the EI equal 90–100. Indeed, in their Table 3 they quote EI = 80 with a GI = 74 for *C. angolensis* and EI = 90–96 with GI = 90 for *C. nigrinus* to give the best fit to the model. In their Figs 2–4, the GI and EI values for each location are equal to each other, indicating that there is no stress incorporated into the model. As the EI is a composite of the GI and the stress indices, it is not possible for the value of EI to exceed that of the GI. Thus, not only are the values of EI quoted by Samways *et al.* unrealistically high, the criteria used to define a good fit to the area-of-origin (EI > 75; GI > 75; MI > 0.6) are inappropriate. In practice there is no reason why the EI in the area of origin should not

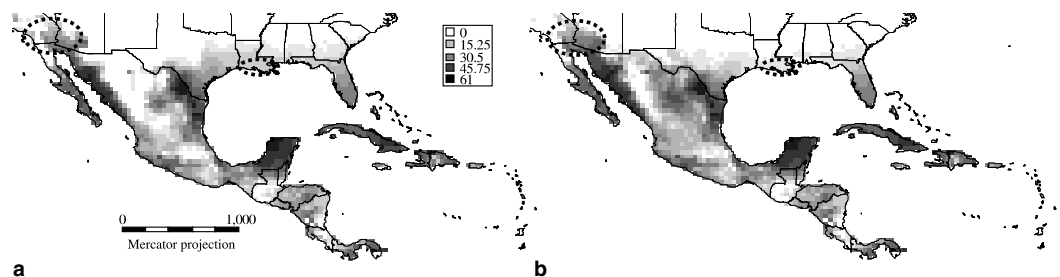


Figure 3 (a) CLIMEX projection of the potential geographical distribution of the ladybird, *Chilocorus cacti* (Linnaeus 1767), in Central and North America using a lethal low temperature stress model. The darkness of shading in each 50 km² grid cell is proportional to the estimated climatic suitability of the area. The areas designated by Fig. 1 in Samways *et al.* (1999) as the 'natural geographical ranges' are shown as ovals with broken lines. (b) CLIMEX projection with a degree-day cold stress model (see text and Table 1 for details).

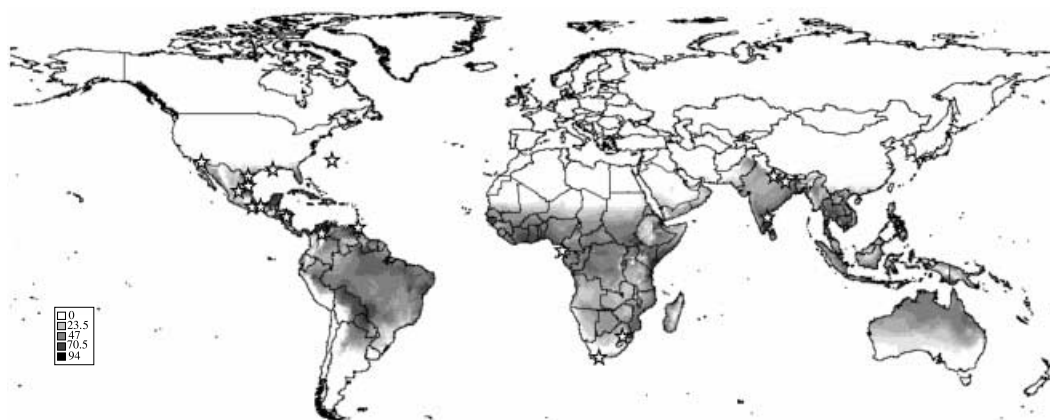


Figure 4 CLIMEX projection of the potential global distribution of the ladybird, *Chilocorus cacti* (Linnaeus 1767). The darkness of each 50 km² grid cell is proportional to the climatic suitability of the area, estimated using the degree-day cold stress model. Stars mark locations where the beetle has successfully established or was recorded outside the range depicted in Fig. 1 of Samways *et al.* (1999).

have been as low as 15–20, which is sufficient to support substantial population densities (Sutherst & Maywald, 1985). The criteria that Samways *et al.* used to define a good fit to the area of origin demonstrates that they did not understand the model. In addition, as shown above, a low Match Climates MI does not necessarily indicate that the matching location is unsuitable for a given species.

A striking feature of the maps provided by Samways *et al.*'s Fig. 1a,b of the 'natural geographical ranges' of each species is the apparently restricted or discontinuous nature of the areas of origin of many of the ladybirds, and the apparent lack of overlap of species. Species to which this applied include: *C. angolensis*, *C. cacti*, *C. circumdatus*, *C. distigma*, *C. hauseri*, *C. infernalis*, *C. rubidus*, *C. schoedtei* and *C. wahlberghi*. This should immediately raise a warning flag that there is either a taxonomic error or that the distributions are incompletely defined or that non-climatic limiting factors are at work. For example, their map (Fig. 1) showed the apparent 'natural geographical range' of

Table 1 CLIMEX model parameters for *Chilocorus cacti* (Linnaeus 1767). Moisture parameters are in units of proportions of soil moisture holding capacity

Parameters	Value
Moisture parameters (proportion of soil moisture holding capacity)	
Lower threshold of soil moisture (SM0)	0.01
Lower limit of optimal range of soil moisture (SM1)	0.1
Upper limit of optimal range of soil moisture (SM2)	1.0
Upper threshold of soil moisture (SM3)	2.0
Temperature parameters (°C)	
Lower threshold of temperature for population growth (DV0)	16.0
Lower optimal temperature for population growth (DV1)	28.0
Upper optimal temperature for population growth (DV2)	38.0
Upper threshold temperature for population growth (DV3)	43.0
Stress indices	
Soil moisture dry stress (proportion of soil holding capacity) (SMDS)	0.001
Weekly rate of accumulation of dry stress (HDS)	-0.0001
Soil moisture wet stress (proportion of soil holding capacity) (SMWS)	2.0
Weekly rate of accumulation of wet stress (HWS)	0.01
Temperature threshold of cold stress (TCS)	7.0 °C
Weekly rate of accumulation of cold stress (THCS)	-0.001
Degree-days (dd) threshold of cold stress (DTCS)*	10.0
Weekly rate of accumulation of cold stress (DHCS)*	-0.0006
Threshold of heat stress (TTHS)	45 °C
Weekly rate of accumulation of heat stress (THHS)	0.001

*Alternative cold stress hypothesis.

C. cacti to be restricted to the New Orleans and southern California areas of the USA, with a large gap between them. This was not consistent with the records in their Table 1 referring to the 'general distribution'/'area-of-origin' of *C. cacti* as being 'Southern N. America, central America, northern S. America, Caribbean Islands'. It is not clear which set of data they used to fit the CLIMEX parameters. Similar inconsistencies were evident with some other species.

I attempted to fit the CLIMEX parameters to describe the ability of *C. cacti* to live in the two contrasting environments of desert in southern Arizona (in irrigated areas) and humid tropical in the south-eastern USA, shown in Samways *et al.*'s Fig. 1b. As is often the case with CLIMEX, in order to include the two environments, the model also includes others that fall into the range of tolerable climatic conditions. It indicated that much of the lower altitude areas (less than *c.* 2000 m altitude) of Mexico were also suitable and included the area from Florida through to western Texas. Thus the model indicated that these areas are climatically favourable for the species, which is not consistent with Samways *et al.*'s Fig. 1b, but is consistent with their Table 1.

A more accurate fit was attempted (Fig 3a), using additional distribution records for Mexico (Gomez *et al.*, 1979; Husband, 1989) and southern Arizona and Texas (Yoder *et al.*, 1999). The model parameter values (Table 1) were still based on very limited observations but provide a guide to the potential range of the species. They indicate that the climate of much of Mexico and the southern USA are climatically suitable for *C. cacti*. It is likely that the Arizona populations rely on irrigated agriculture but no detailed information could be found to support that, hence it was not included in the model. An alternative cold stress hypothesis, based on the need to accumulate 10 degree-days per week above 16 °C (Table 1), gave a similar distribution in North America but included more of the central highlands of Mexico (Fig 3b). This would include the Lagunera region of the States of Coahuila and Durango (Gomez *et al.*, 1979). Without more detailed data, especially on the northern limits of the beetle in the eastern USA, it was not possible to distinguish between the two models. I was unable to check the identity of the specimens referred to in the above publications, so some future verification of their taxonomic status would be desirable.

In contradiction with the records in their Table 1, Samways *et al.*'s Table 2 cited Swezey (1925) as reporting failure of *C. cacti* to establish in California, Mexico and Hawaii. They then used these results in their assessment of the performance of CLIMEX in predicting successful establishment. A review of Swezey (1925) revealed that the failed introduction referred only to Hawaii and that California and Mexico were the *sources* of the material. The Swezey reference to *C. circumdatus* also suffered from the same misinterpretation where the establishment sites were confused with collection sites in South China.

A further search of the literature on *C. cacti* revealed that it occurs widely in Mexico in the high rainfall area around Cordoba in Vera Cruz State (*c.* 18.9 N 97.1 W), and south of Alpujeca, Morelos State (location not traceable but *c.* 19 N 99 W) in the southeast (Husband, 1989) and the Lagunera region of the States of Coahuila and Durango (no further details available) in central and northern Mexico (Gomez *et al.*, 1979). If the species was indeed indigenous to Mexico it would explain the apparently discontinuous range reported by Samways *et al.* (Fig. 1b). Gordon (1985, 1990) also identified the states of southern Arizona, California, Florida and Texas in the USA, and northern South America, Central America and Mexico as having *C. cacti* present.

My interpretation of the CLIMEX parameters for *C. cacti* and *C. stigma*, taken as examples to test the fitting of the CLIMEX model, is that both species are very tolerant of high temperatures and both low and high rainfall, so they are species that have the potential to establish widely if all other non-climatic constraints are removed. This appears to have been the experience with *C. cacti* (Fig. 4), if the results of Samways *et al.*'s Table 2 are accurate. The model identified highly suitable climates in most of India, Africa south of the Sahara, tropical South America, Southeast Asia and northern Australia. Establishment has been confirmed (according to Samways *et al.* citations), in India, the west coast of Central Africa and South Africa. The model identified all sites as being suitable, but the South African sites suffer a greater degree of cold restriction, which makes accurate observations of the northern limit in the eastern USA more pertinent.

Chilocorus stigma, on the other hand, was reported by Samways *et al.* to have failed to establish outside North America. Hence the search for causes of failure of *C. stigma* would most profitably be focused on non-climatic factors. Without any positive establishments it was not possible to test the accuracy of the model in predicting areas with suitable climates for this species. As stated by Sutherst & Maywald (1985) 'discrepancies between observed and predicted distributions can be just as useful as agreements in identifying limiting factors'. Exclusion of climate as a limiting factor is just as useful a measure of success of CLIMEX modelling as is confirmation of that role (Vera *et al.* 2002).

Table 2 Template for CLIMEX species report

Name:
Biology:
Distribution:
CABI CPC Ref: etc.
Comments and literature review related to fitting CLIMEX parameters
<i>Distribution records used to estimate CLIMEX parameter values</i>
<i>Evidence for non-climatic limits to distribution</i>
Physical barriers
Hosts
Vectors
Other species
Artificial environments (e.g. irrigation or glasshouses)
<i>Stress indices</i>
Hot
Cold
Dry
Wet
<i>Climatic Constraints</i>
Obligate diapause
Length of growing season
<i>Growth</i>
Temperature
Moisture
Results
<i>Goodness of Fit</i>
<i>Independent Validation</i>
<i>Source Risks</i>
Geographical
Seasonal
<i>Destination Risks</i>
Geographical
Seasonal
Discussion
References
Species Parameters Table

Samways *et al.* identified host availability, natural enemies and insufficient size of introduced populations as possible factors preventing establishment. They also included short-term effects like insecticide use, weather and microclimates. Quite apart from the issue of non-climatic factors, such as restricted geographical distributions of many of the *Chilocorus* species referred to by Samways *et al.* – if accurate – necessarily imply that most of them incorporate a limited amount of climatic heterogeneity. Thus the options for parameterising any climate-matching model are limited and there is necessarily a high level of uncertainty associated with the model, so projections that are made for other regions, or climate change scenarios, need to be treated with due care, as emphasised by Sutherst & Maywald (1985).

Samways *et al.* also state that their ‘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’. I question whether knowledge of a species biology is in fact necessary if the species response to climatic variables can be inferred from its current geographical distribution using the CLIMEX model. Changes in ranges under climate change are likely to be incremental, even if nonlinear, shifts in species boundaries rather than jumps into quite different climatic environments. Some nonlinear responses may occur where interdependent species respond differently to climate change (Watt *et al.*, 1995; Gutierrez, 2000; Sutherst, 2000b). There has now been sufficient experience with the CLIMEX model to be confident that predictions of species responses, even to quite different patterns of climate in different regions associated with introductions, are usually reliable if the observations are sufficient to parameterize the model and the modelling has been performed competently.

Getting back to the conclusions of Samways *et al.*, it is not logical to conclude from any analysis, using CLIMEX or any other climate-matching algorithm, that ‘only 4 (26.7%) species climatic tolerances could be predicted with 100% certainty’, when the criterion used is the success rate of establishment of introductions. The *Compare Locations* function in CLIMEX describes the *potential* geographical distribution of a species as limited by climate. Given the restricted or discontinuous nature of the distributions of some of the species used by Samways *et al.* (1999), it is most appropriate to conclude either that their records were incomplete, or that non-climatic or handling effects – such as insufficient numbers released, lack of hosts or predation – were responsible for the failure of so many introductions. I emphasize that CLIMEX is a scientific tool that incorporates both ecological understanding and assumptions. It demands that the user understands the scientific basis of the model and the assumptions on which it is built. While fitting parameter values, users are required to test a number of different hypotheses to explain the geographical distribution of the target species. While statistical approaches usually discard or weight ‘outliers’ to reduce their effect, it is more appropriate to take them into account because they are likely to extend the inferred range of tolerance of the species. Technical support for CLIMEX is available at <http://www.climex.ento.csiro.au> and a template to help CLIMEX users avoid omissions of key factors or processes is shown in Table 2.

It is important to emphasize that the CLIMEX model defines the *potential* geographical distribution of a given biological organism in relation to climate. It is a strategic rather than a tactical tool. The role of the CLIMEX software in biological control is, first, to help target collection sites, for as yet unidentified species, using the Match Climates function judiciously, and secondly, to determine whether or not climate will be a limiting factor at a proposed release site for a known agent, using the CLIMEX model in Compare Locations mode. This allows the effects of climate, as opposed to weather at the time of the release, to be taken into account when evaluating the prospects for success and spread of an introduced species. It does not try to explain the outcome of particular events based on climate and conversely, it is not logical to infer species climatic tolerances from the success rate of particular introductions. The issue of range change with climate change is a different question to that addressed by Samways *et al.* It would suffice to say that if the current climatic tolerances of a species can be defined – and there is plenty of evidence to show that they often can be – the task of projecting the effects of incremental changes in climate is just as tractable as that of projecting range expansions under current climate with species that are moved around. In both cases, the climatic environment is changing but for different reasons.

I conclude that the data and results of Samways *et al.* lack accuracy, and their methods and conclusions are neither a critical nor a logical test of the CLIMEX model or of the concept of predicting potential ranges of species based on climate matching.

ACKNOWLEDGEMENTS

Dr Darren Kriticos, Dr Mark Lonsdale, Dr John Scott and Dr Sue Worner reviewed the manuscript and made helpful suggestions.

ROBERT W. SUTHERST

CSIRO Entomology, Long Pocket Laboratories,
120 Meiers Rd, Indooroopilly, Queensland,
Australia 4068
E-mail: bob.sutherst@csiro.au

REFERENCES

- Bruce, D. & Wilson, A. (1998) The extensive spread of heartwater in Zimbabwe since 1975. *Proceedings second international conference on tick borne pathogens at the host vector interface: a global perspective* (eds L. Coons and M. Rothschild), 28 August–1 September 1995, Kruger National Park, South Africa, proceedings and abstracts, pp. 105–112. S.I.: The Conference.
- Cook, W.C. (1925) The distribution of the alfalfa weevil (*Phytonomus pesticus* Gyll.) a study in physical ecology. *Journal of Agricultural Research* (Washington, DC), 30, 479–491.
- Csurhes, S.M. & Kriticos, D.J. (1994) *Gleditsia triacanthos* L. (Caesalpinaceae), another thorny, exotic fodder tree gone wild. *Plant Protection Quarterly*, 9, 101–105.

- DeBach, P. (1964) *Biological control of insect pests and weeds*, 884 pp. Chapman and Hall, Ltd, London.
- Dodd, A.P. (1936) The control and eradication of prickly-pear in Australia. *Bulletin of Entomological Research*, **27**, 503–517.
- Fitzpatrick, E.A. & Nix, H.A. (1970) The climatic factor in Australian grassland ecology. *Australian grasslands* (ed. R.M. Moore), pp. 3–26. Australian National University Press, Canberra.
- Gomez, M.F., Galindo, R.A.I. & Gonzalez, H.N.G. (1979) Fluctuation in the populations of some insects of economic importance in the Lagunera region of the States of Coahuila and Durango. *VII National meeting on biological control: VII Reunion nacional de control biologico*, pp. 10–38. VII. Comite Organizador de la VII Reunion Nacional de Control Biologico, Veracruz, Mexico.
- Gordon, R.D. (1985) The Coccinellidae (Coleoptera) of America North of Mexico. *Journal of the New York Entomological Society*, **93**, 1–912.
- Gordon, R.D. (1990) The Coccinellidae (Coleoptera) of Bermuda. *Journal of the New York Entomological Society*, **98**, 265–309.
- Gutierrez, A.P. (2000) Crop ecosystem responses to climate change: pests and population dynamics. *Climate change and global crop productivity* (eds K.R. Reddy and H.F. Hodges), pp. 353–374. CABI Publishing, Wallingford.
- Hall, M. & Wall, R. (1995) Myiasis of humans and domestic animals. *Advances in Parasitology*, **35**, 257–334. Academic Press, London.
- Husband, R.W. (1989) Two new species of *Coccipolipus* (Acari: Podapolipidae) parasites of *Chilocorus* spp. (Coccinellidae) from Vera Cruz and Morelos, Mexico and Florida and Wisconsin, USA. *Proceedings of the Entomological Society of Washington*, **91**, 429–435.
- Hutchinson, G.E. (1957/8) Concluding remarks. *Cold Spring Harbor Symposia on Quantitative Biology*, **22**, 415–427.
- Julien, M.H., Kerr, J.D. & Chan, R.R. (1984) Biological control of weeds: an evaluation. *Protection Ecology*, **7**, 3–25.
- Kriticos, D.J. & Randall, R.P. (2001) A comparison of systems to analyse potential weed distributions. *Weed risk assessment* (eds R.H. Groves, F.D. Panetta and J.G. Virtue), pp. 61–79. CSIRO, Melbourne.
- Maywald, G.F. & Sutherst, R.W. (1991) *User's guide to CLIMEX, a computerised system for comparing climates in ecology*, 51 pp. Australian CSIRO Division of Entomology Report No. 48, Canberra.
- Mills, N.J. (1990) Biological control of forest aphid pests in Africa. *Bulletin of Entomological Research*, **80**, 31–36.
- Robertson, H.G. (1986) Egg predation by ants as a partial explanation of the difference in performance of *Cactoblastis cactorum* on cactus weeds in South Africa and Australia. *Proceedings of the VI International Symposium on Biological Control of Weeds*, pp. 83–88. Agriculture Canada, Ottawa, Canada
- Room, P.M. & Thomas, P.A. (1985) Nitrogen and establishment of a beetle for biological control of the floating weed *Salvinia* in Papua New Guinea. *Journal of Applied Ecology*, **22**, 139–156
- Samways, M.J., Osborn, R., Hastings, H. & Hattingh, V. (1999) Global climate change and accuracy of prediction of species' geographical ranges: establishment success of introduced ladybirds (Coccinellidae, *Chilocorus* spp.) worldwide. *Journal of Biogeography*, **26**, 795–812.
- Semple, J.L. & Forno, I.W. (1987) Native parasitoids and pathogens attacking *Samea multiplicalis* Guenee (Lepidoptera: Pyralidae) in Queensland. *Journal of the Australian Entomological Society*, **26**, 365–366.
- Smith, C.S., Lonsdale, W.M. & Fortune, J. (1999) When to ignore advice: invasion predictions and decision theory. *Biological Invasions*, **1**, 89–96.
- Sutherst, R.W. (1987) The dynamics of hybrid zones between tick (Acari) species. *International Journal for Parasitology*, **17**, 921–926.
- Sutherst, R.W. (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, R.W. (2000a) Climate change and invasive species – a conceptual framework. *Invasive species in a changing world* (eds H.A. Mooney and R.J. Hobbs), pp. 211–240. Island Press, Washington, DC.
- Sutherst, R.W. (2000b) Climate variability, seasonal forecasting and invertebrate pests – the need for a synoptic view. *Applications of seasonal climate forecasting in agricultural and natural ecosystems. The Australian experience* (eds G.L. Hammer, N. Nicholls and C. Mitchell), pp. 381–397. Kluwer Academic Publishers, Dordrecht.
- Sutherst, R.W. (2001) The vulnerability of animal and human health to parasites under global change. *International Journal for Parasitology*, **31**, 933–948.
- Sutherst, R.W. & Maywald, G.F. (1985) A computerised system for matching climates in ecology. *Agriculture Ecosystems and Environment*, **13**, 281–299.
- Sutherst, R.W. & Maywald, G.F. (1990) Climate change and invertebrate pests in animal industries. *Proceedings of the ASRRC/BRR Workshop on climate change* (November 1989). Australian Bureau of Rural Resources Report No. R/3/90, pp. 7–12.

- Sutherst, R.W., Maywald, G.F. & Bottomley, W. (1991) From CLIMEX to PESKY, a generic expert system for pest risk assessment. *EPPO Bulletin*, **21**, 595–608.
- Sutherst, R.W., Maywald, G.F. & Skarratt, D.B. (1995) Predicting insect distributions in a changed climate. *Insects in a changing environment* (eds R. Harrington and N.E. Stork), pp. 59–91. Academic Press, London.
- Sutherst, R.W., Yonow, T., Chakraborty, S., O'Donnell, C. & White, N. (1996) A generic approach to defining impacts of climate change on pests, weeds and diseases in Australasia. *Greenhouse: coping with climate change* (eds W.J. Bouma, G.I. Pearman and M.R. Manning), pp. 281–307. CSIRO, Melbourne.
- Sutherst, R.W., Maywald, G.F., Yonow, T. & Stevens, P.M. (1999) *CLIMEX. Predicting the effects of climate on plants and animals*, 90 pp. CD-ROM and User guide. CSIRO, Melbourne.
- Sutherst, R.W., Maywald, G.F. & Russell, B.L. (2000) Estimating vulnerability under global change: modular modelling of pests. *Agriculture Ecosystems and Environment*, **82**, 303–319.
- Swezey, O.H. (1925) Records of introduction of beneficial insects into the Hawaiian Islands. *Hawaiian Planter Record*, **29**, 369–376.
- Sykes, M.T., Prentice, C. & Cramer, W. (1996) A bioclimatic model for the potential distributions of north European tree species under present and future climates. *Journal of Biogeography*, **23**, 203–233.
- Vera, M.T., Rodriguez, R., Segura, D.F., Cladera, J.L. & Sutherst, R.W. (2002) Potential geographical distribution of the Mediterranean fruit fly, *Ceratitidis capitata* (Diptera: Tephritidae), with emphasis on Argentina and Australia. *Environmental Entomology*, **31**, 1009–1022.
- Waterhouse, D.F. & Sands, D.P.A. (2001) Classical biological control of arthropods in Australia. *ACIAR Monograph*, **77**, 560.
- Watt, A.D., Whittaker, J.B., Docherty, M., Brooks, G., Lindsay, E. & Salt, D.T. (1995) The impact of elevated atmospheric CO₂ on insect herbivores. *Insects in a changing environment* (eds R. Harrington and N.E. Stork), pp. 198–219. Academic Press, London.
- Williamson, M. & Fitter, A. (1996) The varying success of invaders. *Ecology*, **77**, 1661–1666.
- Worner, S.P. (1991) Use of models in applied entomology: the need for perspective. *Environmental Entomology*, **20**, 768–773.
- Yoder, J.A., Houck, M.A., Goodin, B.R. & Smith, J.A. (1999) Maintenance of water balance in the twice-stabbed ladybird beetle, *Chilocorus cacti* (Coleoptera: Coccinellidae), despite heavy infestation by the mite, *Hemisarcoptes cooremani* (Acari: Acariformes). *International Journal of Acarology*, **25**, 337–340.
- Yonow, T. & Sutherst, R.W. (1998) The geographical distribution of the Queensland fruit fly, *Bactrocera (Dacus) tryoni*, in relation to climate. *Australian Journal of Agricultural Research*, **49**, 935–953.

BIOSKETCH

Bob Sutherst is an ecologist with interests in applying generic population modelling to risk assessments and management of pests, diseases and weeds, with recent emphasis on global change and invasive species. He is interested in exploiting the information available in spatial data to accelerate understanding of the climatic requirements of species in order to provide a context for site-specific studies. He led the development of the CLIMEX model.