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Concept paper

Predicting population dynamics of weed biological control agents: science or gazing into crystal balls?

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Abstract Various factors can influence the population dynamics of phytophages post introduction, of which climate is fundamental. Here we present an approach, using a mechanistic modelling package (CLIMEX), that at least enables one to make predictions of likely dynamics based on climate alone. As biological control programs will have minimal funding for basic work (particularly on population dynamics), we show how predictions can be made using a species geographical distribution, relative abundance across its range, seasonal phenology and laboratory rearing data. Many of these data sets are more likely to be available than long-term population data, and some can be incorporated into the exploratory phase of a biocontrol program. Although models are likely to be more robust the more information is available, useful models can be developed using information on species distribution alone. The fitted model estimates a species average response to climate, and can be used to predict likely geographical distribution if introduced, where the agent is likely to be more abundant (i.e. good locations) and more importantly for interpretation of release success, the likely variation in abundance over time due to intra- and inter-year climate variability. The latter will be useful in predicting both the seasonal and long-term impacts of the potential biocontrol agent on the target weed. We believe this tool may not only aid in the agent selection process, but also in the design of release strategies, and for interpretation of post-introduction dynamics and impacts. More importantly we are making testable predictions. If biological control is to become more of a science making and testing such hypothesis will be a key component.

Key words biogeography, climate, CLIMEX, day degrees, modelling, phenology.

INTRODUCTION

The population dynamics of introduced biological control agents of weeds should be relatively easy to predict. The 'host plant', a weed, is by definition abundant and widespread (otherwise we would not be doing biological control). A host-specific phytophagous insect has been selected, mass reared, released and established ostensibly with few natural enemies of its own. The expectation is that the introduced agent should 'take off', increase rapidly in abundance and as a consequence of the feeding damage inflicted 'do the job' – namely the abundance of the weed should decline and the two species should exist in some new stable equilibrium, as is usually depicted in the textbooks (Fig. 1) (e.g. Caughley 1976)

When the scenario outlined above occurs the results are spectacular. A number of such cases have been documented and are of course the stuff of textbooks. Classic success stories include prickly pear and the pyralid *Cactoblastis cactorum* (Berg, 1885) (Dodd 1940), and Salvinia and *Cyrtobagous salviniae* Calder & Sands (Room 1986). The proportion of weed biological control campaigns that are this successful is in fact low. In most cases there is little assessment of either the agent or its impact beyond the establishment phase. Weed biological control campaigns have been reviewed by various authors over the years (Julien *et al*. 1984; McFadyen 1998) and, generally, fewer than 10% look anything like Figure 1. In fact, the population dynamics and subsequent impact on the target weed can vary greatly within and between biocontrol agents. Ignoring the outright failures where the introduced agent goes extinct, the temporal dynamics of introduced agents can range from just hanging in there – the agent remains localised and rare – to rapid outbreak and decline, to periodic localised outbreaks; in fact all the types of dynamics one would expect for a phytophagous insect (Myers 1987).

The holy grail of biological control (and perhaps ecology) is to be able to predict the expected population dynamics of the introduced agent (or any organism for that matter) (van Klinken *et al*. 2002). Most 'predictive' models in biological control are constructed around 'predator–prey' theory with a pair of equations describing the interaction and dynamics of the weed (W_t) and insect (N_t) populations:

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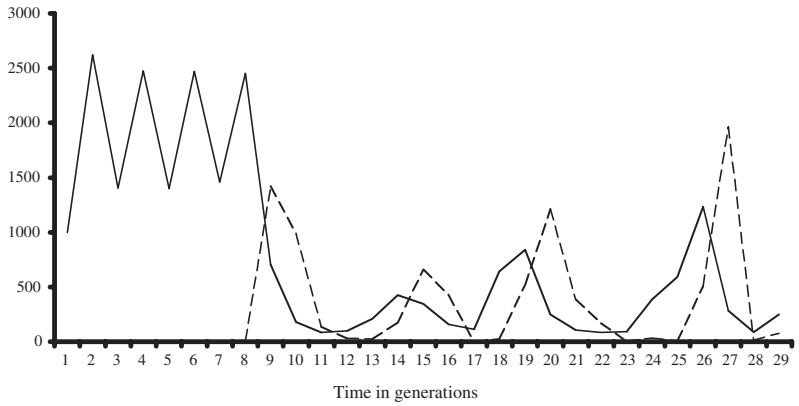

Fig. 1. Expected population dynamics if an introduced biological control agent manages to reduce the abundance of the target weed. The agent is introduced at generation 8, the weed population collapses by generation 10 and the two populations subsequently fluctuate at a much lower equilibrium level.

$$W_{t+1} = f_1(W_t)\cdot W_t \cdot f_2(W_t, N_t)$$

$$N_{t+1} = N_t \cdot f_3(W_t, N_t)$$

where $f_1(W_t)$ is a function that describes the growth rate of the weed population and may include various aspects of weed biology and life history, $f_2(W_t, N_t)$ is the survival and/or seed set of weeds when confronted by N_t insects, and $f_3(W_t, N_t)$ is the growth rate of the herbivore when feeding on the weed (e.g. Caughley 1976; Buckley *et al*. 2003, 2004, 2005).

To describe population dynamics using a pair of predator–prey equations requires relatively few parameters: usually some growth rates for each of the protagonists, some density dependent terms, search efficiency and so forth. Although useful in strategic terms (Buckley *et al*. 2004) such models rarely capture the actual population dynamics post introduction, let alone of source populations.

Processes in insect–plant interactions are more complex than depicted by the pair of equations above. Population growth rate of a weed, say r, just tells us the potential speed of change. Realised r is affected by many things other than density and a single herbivore! For insects most models focus on mortality, its level, causes and density relations. In practice the dynamics of the weed, the phytophagous insect and their interaction are influenced by climate in many ways (as well as soil type, plant quality, distribution, management practices, etc.). In any consideration of the different factors influencing phytophage distribution and abundance (namely its population dynamics), one needs to consider as a minimum set of interacting components: the host plant(s), the phytophage of course, its natural enemies and other phytophages that feed on the plant (Fig. 2). Climate is the main focus of this paper as it is a 'primary driver' for each of the components and their interactions (Fig. 2; Andrewartha & Birch 1954; Barbosa & Schultz 1987; Walter & Zalucki 1999).

Working out the population dynamics of a species can keep a large research group going for a long time. This is generally not possible in a biological control program. Here we outline a mechanistic climate-modelling approach that uses a minimum amount of data based on a species geographical distribution. We infer the species response to climate and then generate the potential effect of climate on temporal dynamics (Box 1, Fig. 3). In effect we predict what we might expect population dynamics to be assuming only climate is limiting.

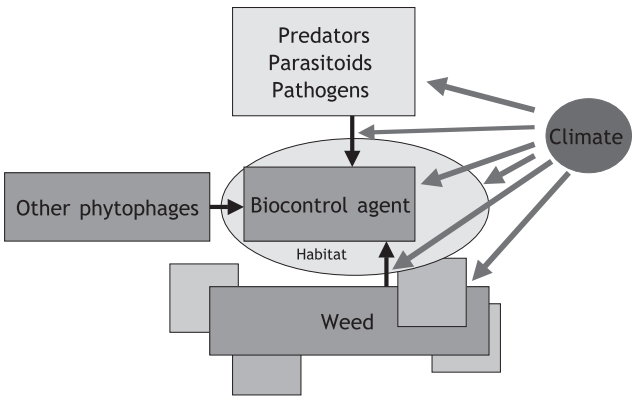

Fig. 2. The basic interacting components that need to be considered in the population dynamics of a phytophagous biocontrol agent. Climate is the primary driver as it affects each component directly as well as their interactions (not all arrows shown).

In addition, we outline the data requirements that researchers need to gather during the survey phase (see Goolsby *et al*. 2006) and in the quarantine-testing phase of a biological control program. Such an approach we believe would be useful for selecting agents, timing their introductions, interpretation of outcomes and of course making predictions ahead of time. The release of the agent, should the program get to this stage, and subsequent monitoring can test the hypothesis (or model prediction).

Of course, population dynamics of the introduced agent post introduction is only one component in determining success of the program (van Klinken & Raghu 2006). Any weed biocontrol program needs to get at the population dynamics of the target weed, itself influenced by climate, and how feeding impacts on its abundance (e.g. Kriticos *et al*. 1999; Buckley *et al*. 2003, 2004, 2005; Kriticos 2003; Raghu *et al*. 2006).

ESTIMATING THE EFFECTS OF CLIMATE BASED ON WHERE ANIMALS ARE FOUND

Physiologists have long been aware of the effects of extreme variation of climatic variables, such as temperature and

Box 1 Inferring the ecological requirements of a species in climate (niche) space based on species geographic distribution

Various approaches have been used to infer the ecological requirements of a species in climate (niche) space based on species geographic distribution (Sutherst & Maywald 1985; Peterson 2003; Zalucki & Furlong 2005). Here we use the climate-modelling function called 'compare locations' (to differentiate from the climate-matching function that is sometimes used) within CLIMEX, a software package developed by Maywald and Sutherst (1991). If climate is one of the main determinants of where a species is likely to be found, we might expect a strong influence of climate variability on both spatial and temporal variation in abundance. CLIMEX is generally used to predict the suitability of a site for a species based on long-term average climate and the species estimated responses to temperature and moisture requirements and so forth (Table 1, see text for details). If we have the long-term daily (or weekly) weather data for a site we can use the estimated species response to climate variables (Fig. 3a), to infer the variation in suitability (variation in the various CLIMEX indices) and hence species abundance at the site over time (Fig. 3b). Essentially we are generating a model of likely temporal abundance based on climate alone, using information on a species geographic distribution to derive its responses to changing climatic conditions (Fig. 3a).

moisture (variously measured), on essential physiological processes (e.g. thermoregulation, osmoregulation and growth), and of the consequences of such extremes for the development, survival and reproduction of organisms. Such work is useful in delineating the potential geographical range, based on the effect of extremes on the most sensitive stages (Liebig's Law of the minimum; e.g. Krebs 2001).

Non-physiologists have used various approaches to estimate the ecological consequences of climate. Climograms or klimadiagrams (two dimensional plots of climate variables against each other; see Walter & Lieth 1960) have been used to infer possible suitable sites, based on similarity to known good sites (Wapshere 1974, 1983, 1993; Dennill & Gordon 1990). A more quantitative approach has been taken using the 'climate-matching' function within CLIMEX (Kleinjan & Scott 1996; Adair & Scott 1997). In a variation on this approach, Rogers (1979) estimated mortality rates due to climate from an analysis of a long series of abundance data for Tsetse fly, *Glossina* sp. He plotted in climate space (mean monthly saturation deficit vs. mean temperature) where reproduction exceeded mortality and so mapped a species' potential distribution.

A more sophisticated climate-matching approach is to use multivariate statistical techniques to infer, from georeferenced distributional data, the climatic factors that correlate with the species' range. These approaches essentially determine the 'climate envelope', a set of usually arbitrary meteorological values that statistically encompass the locations where a species currently exists, or was known to exist from collection records. The meteorological variables chosen tend to be arbitrary, and not necessarily related to biological processes that in fact influence survival, reproduction and movement. In addition, they may have arbitrary temporal resolution, for example, temperature in the hottest month, range of temperature in the coldest quartile and so forth. As many collection records will be from sites without meteorological recording stations, the various methods usually rely on interpolated climate surfaces. Such climate surfaces may be used within CLIMEX, although they are not essential.

A number of methods for fitting climate envelopes are available. These methods vary in both the climate variables used and the way in which envelopes are defined. Some use standard statistical techniques, such as generalised linear modelling (Nicholls 1989). Others use computer programs that incorporate specialised algorithms. Such programs include HABITAT (Walker & Cocks 1991), BIOCLIM (Busby 1991) and DOMAIN (Carpenter *et al*. 1993). Some methods (e.g. generalised linear modelling and HABITAT) can incorporate variables such as soil type and vegetation type, in addition to climate variables, when defining 'envelopes'.

The ability of these statistical and rule-based approaches to model species distributions and to make meaningful predictions has been criticised (Kriticos & Randall 2001; Sutherst 2003; although see Robertson *et al*. 2003; van Klinken *et al*. 2003). An alternative approach is to explicitly incorporate the physiological processes that interact with climate and thereby influence the organism's distribution and abundance. The software program CLIMEX (Maywald & Sutherst 1991; see Sutherst & Maywald 2004 for the most recent version) is, as far as we know, the only readily accessible and user-friendly modelling package that integrates physiological processes, and hence produce predictions that are more likely to be biologically meaningful and predictive. It therefore lends itself to assisting agent selection decisions, and is the climate-modelling tool that we focus on in this paper.

THE CLIMEX APPROACH

CLIMEX has been used extensively in biological control programs and pest risk analysis to predict potential distributions of Diptera (Sutherst *et al*. 1989, 2000; Yonow & Sutherst 1998), Hymenoptera (Spradbery & Maywald 1992; Sutherst & Maywald 2005), Coleoptera (Julien *et al*. 1995; Heard & Forno 1996; Samways *et al*. 1999), Homoptera (Hughes & Maywald 1990; Scott & Yeoh 1999; Wharton & Kriticos 2004), Heteroptera (Steinbauer *et al*. 2002), Lepidoptera (Matsuki *et al*. 2001; Zalucki & Furlong 2005),

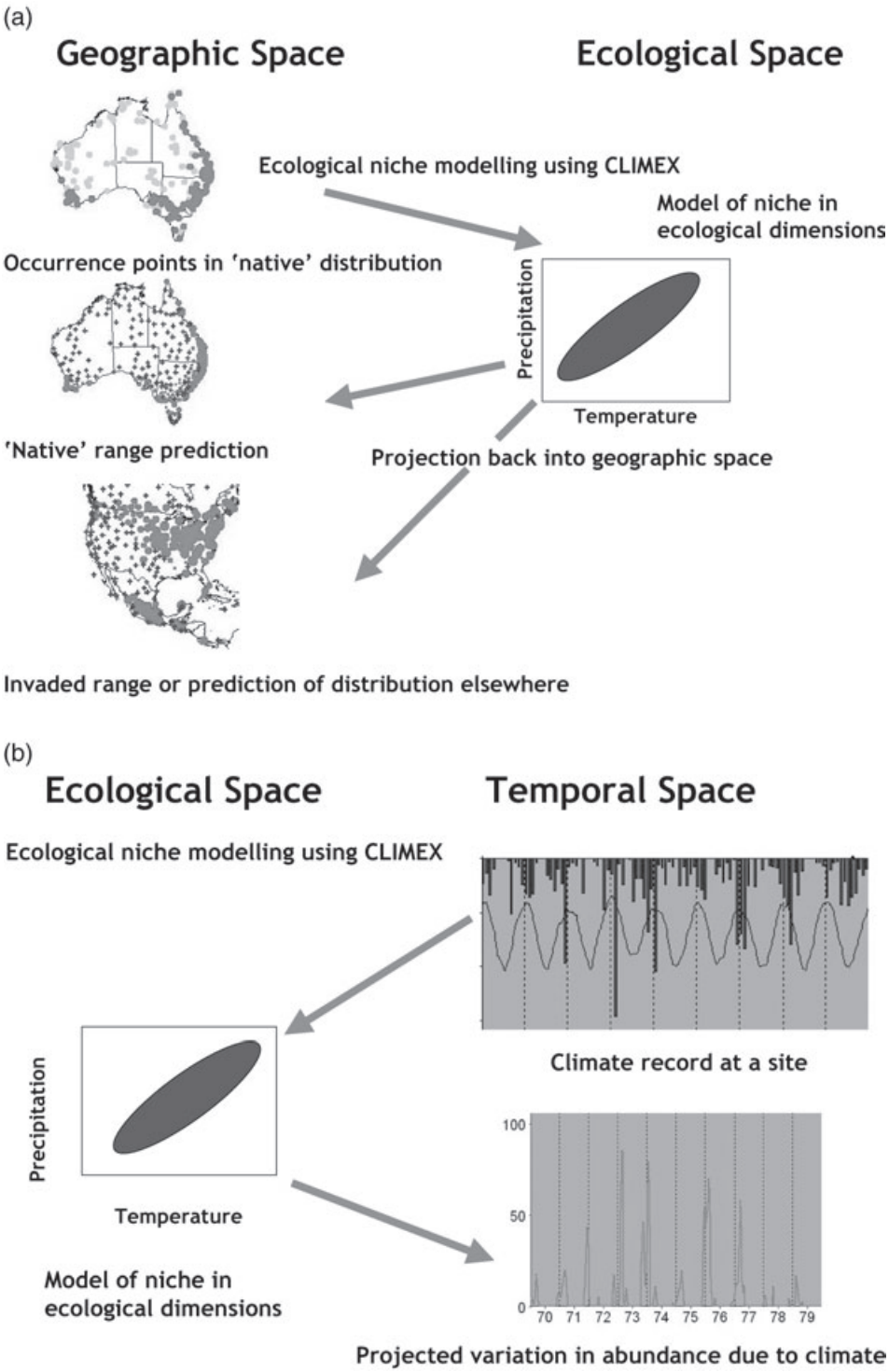

Fig. 3. Diagrammatic representation of the processes involved in developing ecological climate niche models that predict the geographical range of a species (a) and temporal variation in abundance at sites within that range (b). We have used the observed geographical range of a closely related species (*Danaus petilia*, light dots) to indicate negative records for *Danaus plexippus* (monarchs, dark dots) in Australia. CLIMEX was then used to undertake ecological niche modelling (see text) to generate estimates of parameters that define suitable climate space and these were then used to predict the occurrence of the species in Australia (dots indicate positive ecoclimatic index (EI) values, crosses indicate the site's climate is not suitable) and in North America. The same set of parameters that define suitable climate space can then be used in conjunction with the recorded climatic variation at any site to generate a temporal variation in EI values.

plants (McFadyen & Skarratt 1996; Kriticos *et al*. 2003) and a vertebrate (Sutherst *et al*. 1995). However, this method has not yet been used for prioritising weed biocontrol agents (van Klinken *et al*. 2003), possibly because the data required are perceived to be too difficult and costly to obtain (McClay 1996) and a lack of confidence in predictions among practitioners. The latter criticisms can only be overcome if the approach we outline is put to use and actually tested.

CLIMEX assumes that individuals at a given location experience two seasons during a year: one favourable to population increase and the other less favourable to the species survival or persistence, due to the seasonality in climate in most locations. A growth index (GI), analogous to population growth rate, describes the potential of the population to increase at a location during the favourable period. The GI, scaled between 0 and 1, is calculated weekly, and is a product of temperature (TI) and moisture indices (MI), namely, GI = TI * MI. For

both the TI and MI, there is a range of conditions of temperature and moisture over which growth is maximal. Either side of the optimum range growth decreases. Above some upper threshold and below a lower thresholds growth ceases (Table 1).

Persistence at a location is modelled by four stress indices (SI), describing the species response to extreme cold, heat, dry and wet conditions, and if needed their interactions (SX); being cold-dry, cold-wet, hot-dry and hot-wet stresses. The SI are accumulated at some rate whenever conditions exceed a specified threshold level (Table 1).

A measure of the relative suitability of a location is summarised in a single annual ecoclimatic index, EI, scaled to 100, namely,

$$EI = 100\Sigma GI/52 * SI * SX$$

where 52 is the number of weeks in a year.

Indices are calculated on a weekly basis for each location using standard meteorological information. A location's long-term monthly average maximum and minimum temperatures, rainfall and humidity values are used as inputs to calculations of the various indices. Areas where the EI is positive are suitable for a species, and the larger the value of EI, the more suitable the location. The values for parameters that describe the TI and MI components of growth, and the various SI and their SX can be estimated from laboratory or field studies (Table 1, see below). Unknown or poorly measured values are estimated by an iterative procedure that involves comparing the predicted distribution with the observed geographical distribution, relative abundance and seasonal phenology. The results of such parameter tuning can be validated by comparing the predicted and observed species distribution to an area not used for the procedure (see examples of CLIMEX use above). Apart from the CLIMEX manual (Sutherst *et al*. 1999), a good exposition of the parameters and a worked example of using CLIMEX for *Bactrocera tryoni* (Froggatt) can be found in Yonow and Sutherst (1998).

Data requirements for a CLIMEX fit

The base data for a CLIMEX model are the geographical distribution of the species being studied. This information is not always available but collection records for specimens held in museums are a useful start (e.g. Zalucki & Rochester 1999, 2004; Dingle *et al*. 2005) and should be part and parcel of the survey process in selecting an agent (Goolsby *et al*. 2006). In some cases published information may be sufficient to generate a useful CLIMEX model (see Matsuki *et al*. 2001).

CLIMEX essentially calculates an index of suitability for a site based on the species response to temperature and moisture. Apart from knowledge of a species geographical distribution, additional information on relative abundance across this range, seasonal phenology (Scott 1992) and if available a species response to one or more variables (e.g. temperature) from laboratory studies greatly add to the parameter fitting process. The latter is particularly useful because it reduces the number of parameters being estimated.

Museum specimens and their label data, if available, are likely based on haphazard collection records. Although a good start, they give positive collection sites only and unless these are extensive and cover the geographical range of a species they give no idea of where a species is not found, as neither negative data nor collecting effort is routinely recorded with collected specimen data. In any systematic home-range survey as part of a biological control program researchers should not only record where potential target species are found but also where they are not found. Precise latitude, longitude and altitude information should be recorded for each sampling site. These will enable the researchers to relate their sites to the climate at the nearest recording station or to interpolated climate surface data.

To be able to infer the effects of climate extremes on a species range, researchers should aim to systematically sample across the climatic distribution of the host plant. For example, transects that traverse the geographical range both north–south and east–west may include the effects of climatic extremes (too cold, hot, dry and/or wet). Similar data could sometimes be obtained by sampling across a number of altitudinal gradients, including both wet and rain-shadow sides of mountain ranges. At a minimum the researcher will record presence and absence data for each sampling site. With more effort the researcher may be able to estimate absolute or at least relative abundance of the potential target species at each sampling site. This will enable the researcher to better estimate the effect of climatic variables. The assumption is that the species will be present (and relatively more abundant) in regions where climate is suitable, becoming relatively rare (or absent) in regions where climate becomes extreme or limiting (too hot, too dry, too cold, too wet). Such systematic and quantitative sampling should be part of any survey effort.

At selected sites it would be useful to sample the abundance of the target species (and preferably all life stages) on a regular basis over at least a year. The sampling interval will of course depend on the species life history. If this is not known then sampling should be on a regular basis and as frequently as possible (e.g. once a week). Such sampling will be useful for a number of reasons but basically it enables the researcher to infer the species seasonal phenology; the times of year when a species is present or absent, and if present, how many generations occur during 'the season'. If this sort of sampling is possible at sites across a range of climatic zones then various phenologies may be expected. At each site we assume there is a period when climate is most suitable for population persistence and times when conditions are not suitable.

If the species is absent at some times of the year the researcher may suspect either a diapause stage, or that the species dies out and migrates back from elsewhere when conditions improve. In either event these data will be useful for a CLIMEX fit as predicted seasonal EI, etc. can be compared with observed species presence (or changes in abundance) and parameters adjusted as required.

A CLIMEX fit requires estimates for the eight parameters that define the response to temperature and moisture. If stresses are included then around 20 parameter values would

Table 1 Some of the more important CLIMEX parameters and how to obtain estimates for them. All parameters can be estimated by fitting to field data. Alternate data sources are listed. For plants a light index would be included (see Sutherst *et al*. 1999)

Environment variable or process	Parameter	Definition	Description and data source
Temperature	DV0	Lower temperature threshold; below this temperature the population will not grow	The temperature (T) range DV0 < T < DV3 in which a species can live and the population grow. Laboratory experiments that estimate rate of increase or its components (mortality, reproduction or development rate) at a wide range of temperatures can be used to provide initial estimates
	DV1	Lower optimum temperature	
	DV2	Upper optimum temperature; between DV1 and DV2 population growth is maximal	
	DV3	Upper temperature threshold; above this temperature populations will not grow	
Moisture	SM0	Lower soil moisture threshold; below this temperature the population will not grow	The soil moisture (SM) range over which a species can live and the population grow. The assumption is that SM determines microclimate and moisture content of vegetation which in turns determines population growth. Field observations may give an indication as to whether a species prefers moist or dry conditions. Laboratory experiments that estimate rate of increase or its components (mortality, reproduction or development rate) at a wide range of humidities can be used to provide initial estimates
	SM1	Lower optimum soil moisture	
	SM2	Upper optimum soil moisture between SM1 and SM2 population growth is maximal	
	SM3	Upper soil moisture threshold; above this soil moisture populations will not grow	
Diapause	DPD0	Diapause induction day length; the average weekly day length that induces diapause	Diapause induction, duration and termination is usually studied under controlled laboratory rearing experiments. Inferences may be drawn from field observations
	DPT0	Diapause induction temperature; average weekly minimum (for winter) or maximum T (for summer) that induces diapause	
	DPT1	Diapause termination temperature; average weekly minimum (for winter) or maximum T (for summer) that terminates diapause	
	DPD	Diapause development days; minimum number of days required to complete diapause. If this minimum is not achieved the species cannot survive diapause and annual growth index is set to zero	
	DPSW	Diapause season; either summer or winter	
Cold stress	DTCS	Threshold number of degree-days above DV0 at which cold stress begins to accumulate	Some indication of lower temperature limits may be obtained from laboratory rearing experiments. Geographic regions or times of the year where a species becomes rare or absent and that experience cold conditions can be used to fit parameter values
	DHCS	Rate at which cold stress accumulates when the threshold number of degree-days above DV0 (DTCS) is reached	
	TTCS	Temperature threshold at which cold stress begins to accumulate	
	THCS	Rate at which cold stress accumulates when T_{min} < TTCS	
Heat stress	DTHS	Threshold number of degree-days above DV3 at which heat stress begins to accumulate	Some indication of high temperature limits may be obtained from laboratory rearing experiments. Geographic regions or times of the year where a species becomes rare or absent and that experience extreme heat conditions can be used to fit parameter values
	DHHS	Rate at which heat stress accumulates when the threshold number of degree-days above DV3 (DTHS) is reached	
	TTHS	Temperature threshold at which heat stress begins to accumulate	
	THHS	Rate at which heat stress accumulates when T_{max} > TTHS	
Dry stress	SMDS	Soil moisture threshold at which dry stress begins to accumulate	Usually fitted. SMDS will usually be set to SM0
	HDS	Rate at which dry stress accumulates when SM is below SMDS	
Wet stress	SMWS	Soil moisture threshold at which wet stress begins to accumulate	Usually fitted. SMWS will usually be set to SM3.
	HWS	Rate at which wet stress accumulates when SM is above SMWS	
Limiting conditions	PDD	Length of growing season	The number of degree-days above DV0 required to complete a generation (from egg to, say, reproductive adult). Typically estimated from temperature and rate of development studies

be required. A fully parameterised model may require up to 40 parameters (Table 1). The more of these parameters that are known *a priori*, the better. For many well-studied insect species the effect of at least temperature on bionomic characters are reasonably well known from laboratory or field studies (e.g. Liu *et al*. 2002), although it is surprising how even for pest species this may not be the case.

If a researcher is beginning to believe a surveyed species may be a useful control agent, then they will likely attempt to rear the species under laboratory or semi-field condition in the home-range survey component. Depending on the facilities available the researchers should attempt to rear the species at more than one temperature. At a minimum at least four temperatures that span the likely range of temperatures the species may experience should be used; as a first guess these might include 15, 20, 25 and 30°C. Such studies can use standard procedures to estimate developmental parameters such as day-degree requirements and developmental thresholds (e.g. Zalucki 1982; see below). Obviously the more temperatures that can be investigated the more that can be inferred (high and low temperature stress, optimum temperatures). This requires resources that may not be available.

An alternative method to obtain temperature-dependent developmental parameters in the laboratory is to do so in the field. As part of the regular sampling for seasonal phenology (above), one could increase sampling effort (sample more regularly) and record the temperatures actually experienced by organisms being observed in the field. If additional experimental manipulation is possible, then subjecting some cohorts of field animals to higher temperatures (greenhouse effects) and others to cooler conditions (e.g. shading) will enable the investigator to gather developmental data on animals under a wider range of fluctuating field temperatures over the season (e.g. Mohandass & Zalucki 2004). Such an intense study is not only useful for data on seasonal phenology and life history, but also provides data that will enable the calculation of developmental parameters using the following relationship:

$$t = \text{end of stage}$$

$$\Sigma f(T(t))\,\Delta t = 1,$$

$$t = \text{start of stage}$$

where $f(T)$ is a function that relates rate of development to temperature, and $T(t)$ is the temperature record experienced over time t from the start of observation (say newly laid eggs found or placed in the field) to the end (say completion of the egg stage, emergence of adults, or whatever stage is of interest to the investigator; the increased frequency of sampling is needed to identify the time when a stage starts and ends). By definition, the organism has completed development when the summation (above) is completed over the duration of the stage(s) being observed equals one (1). This enables the investigator to use various statistical techniques to estimate the parameters of any specified rate of development function $f(T)$. An example of this approach can be found in Dallwitz and Higgins (1978) (see Dallwitz 1984 for an example of the application of this approach). The approach enables researchers to estimate rate of development from field data, which has certain advantages over laboratory-based studies.

The rate of development function, derived either from laboratory or from field studies, enables the researcher to estimate a number of CLIMEX parameters, for example, DV0, and possibly DV1, DV2 and DV3 as well as PDD, and some of the temperature stress parameters (Table 1). This will reduce the number of parameters that need to be subsequently fitted by iteration. In addition, this development rate function could be used in a simple climate-driven phenology model (see beyond CLIMEX below). Such a phenology model can be very useful to both interpreting field data, determining if diapause is suspected as well developing alternate mechanistic models for the effects of climate on the target species (see Zalucki & Rochester 2004).

USING CLIMEX TO PREDICT TEMPORAL DYNAMICS: A CASE STUDY

To illustrate the process we use monarch butterflies, *Danaus plexippus* L., as a case study (Box 1, Fig. 3). Similarly, Scott and Yeoh (1999) develop a CLIMEX model that helps account for year-by-year changes of abundance of an aphid, accidentally introduced into Australia.

Although not deliberately introduced for biological control, monarchs spread across the South Pacific in the 1800s and reached Australia in 1870 (Clarke & Zalucki 2004; Zalucki & Clarke 2004). Their numbers reached high levels on some islands and they exerted some control over imported milkweed hosts (e.g. Blakley & Dingle 1978).

Zalucki and Rochester (1999) used distribution data from Museum specimens for monarch butterflies in Australia to estimate the CLIMEX parameters and found a reasonable 'prediction' of the monarch's seasonal distributions in North America (Fig. 4), its home range. Using the same set of CLIMEX parameters they projected the potential worldwide distribution of monarchs (Fig. 5a), as has been done for other species. This prediction encompasses known distributions (Fig. 5b), including that of *D. p. erippus* in South America and the Pacific. Other areas, such as central and southern Africa, western Europe and parts of Asia, appear suitable. Either the monarch has not yet been introduced to these areas, or the number arriving has been too few to establish, or other limiting factors, such as an absence of milkweed, may prevent successful establishment. A similar process could be undertaken for any biological control agent.

To illustrate the changing suitability of climate for population increase over years we simulate the EI for Amberley (latitude 27°38′S; longitude 152°43′E), a site within the core range of monarchs in Australia (in south-east Queensland), using 20 years of climatic data. Monarchs are predicted to fluctuate widely in abundance here (Fig. 6) even though the site is within the core of the species distribution in Australia (see Zalucki & Kitching 1984). Seasonally the species is expected to build up from a low during winter peaking in summer, which agrees with field observations (Zalucki &

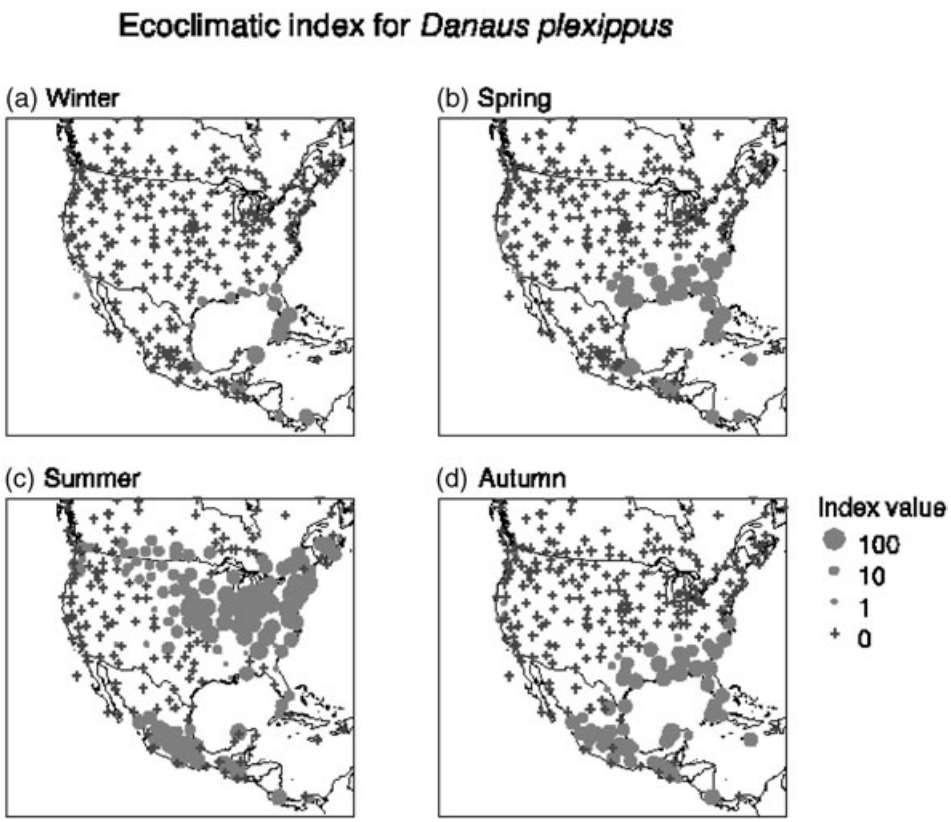

Fig. 4. The predicted distribution of monarchs in North America using CLIMEX parameters in Zalucki and Rochester (1999) for (a) winter, (b) spring, (c) summer and (d) autumn. Locations marked with a cross have indices of zero. The larger the index value, the more suitable the location for the species.

Kitching 1984; Zalucki *et al*. 1993). Winters had an average EI value of 4, with 41% of years as low as zero; spring values average 23 (with 9% of years having a zero value), summer EIs were around 30 (9% zero) and autumn EIs were around 26 (9% zero). Among years abundance can vary by up to 500%, from a low during 1965, a very dry year (EI = 6), to a high in 1983 (a comparatively wet year with EI = 30). The basic point we make with this analysis is that when interpreting changing abundance of a species we have to first take into account the influence of climate on its potential abundance. Deviations from this prediction can then be used as evidence that further factors need to be considered. Thus, apparent declines in some years should not immediately be attributed to factors such as herbicide treatment of milkweeds, or apparent deterioration of overwintering sites, as has been speculated for North America. They may simply reflect normal variation in abundance, due to normal climatic variation, from year to year.

Zalucki and Furlong (2005) developed a CLIMEX model for *Helicoverpa* species in Australia using distribution data from Zalucki *et al*. (1986, 1994), Gregg *et al*. (1995), Matthews (1999), and literature values for various parameters. The predicted recent changes in abundance of *Helicoverpa* sp. at Narrabri (in north-central New South Wales) based on a CLIMEX temporal variation model suggest numbers should have declined. This coincides with increased area of Bt Cotton. Thus, two hypotheses can be proposed for the decline in *Helicoverpa* pest status and simply viewing trends in numbers will not decide between the two (Zalucki & Furlong 2005).

GOING BEYOND CLIMEX

Although climate may be a primary driver of insect abundance and the focus of this contribution other components will need to be considered in any process of agent selection and predicting population dynamics (Fig. 3). Samways *et al*. (1999) suggest that phenology, host type and availability, presence of natural enemies and hibernation sites play a varying role over and above climate, in determining whether a species will establish at a new locality, and the level of abundance it will attain; but see Sutherst (2004) for a critique of this paper.

Synchrony with host, and host quality

After the direct effects of climate, host plant attributes are likely to be the key factors influencing phytophage dynamics. A plant that has become a weed is unlikely to be limiting for a herbivore in terms of abundance of resource. Nonetheless, synchronicity with hosts is likely to be critical when hosts are temporally limiting, such as for annuals, and where feeding is restricted to plant parts such as flowers and seeds. For both uni-voltine and multi-voltine species this means that the agent may need mechanisms to survive periods when their food source is rare or absent, and to respond rapidly to potentially narrow bursts of high resource availability (van Klinken 2005). This can be particularly challenging when seeking agents that will perform well in more extreme environments, such as where plant growth and reproduction can be cued to specific environmental cues such as day length changes, and in arid regions where annual variation in plant abundance can be dramatic.

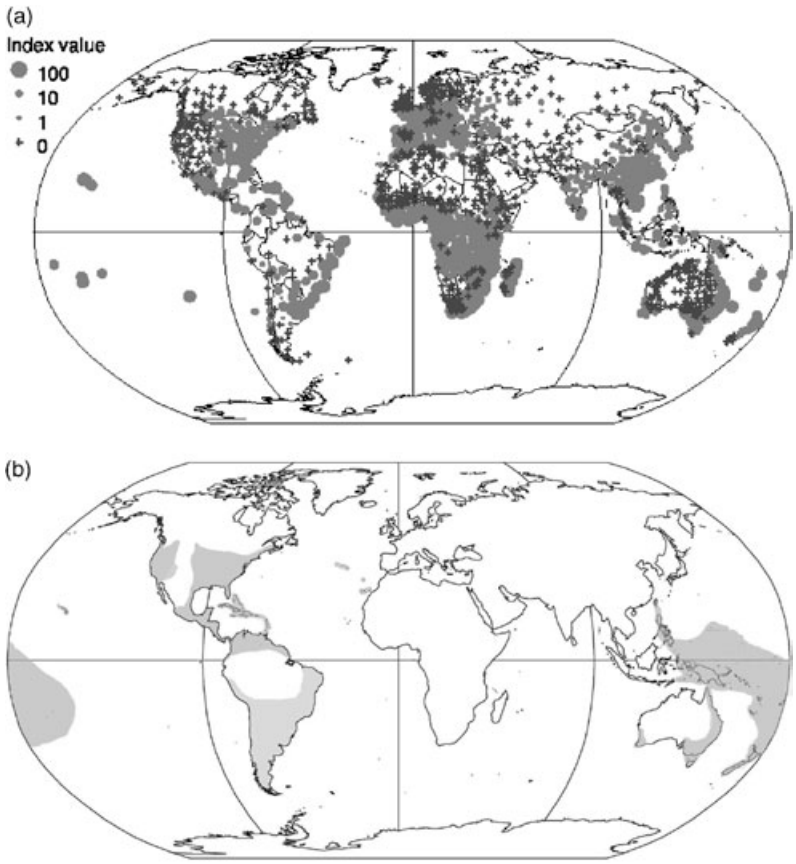

Fig. 5. The predicted worldwide distribution of monarchs based on positive values of ecoclimatic index, EI. Locations marked with a cross have EI values of zero (a) and the known geographical distribution of monarchs (dark shading) and the closely related *Danaus plexippus erippus* (light shading) (b).

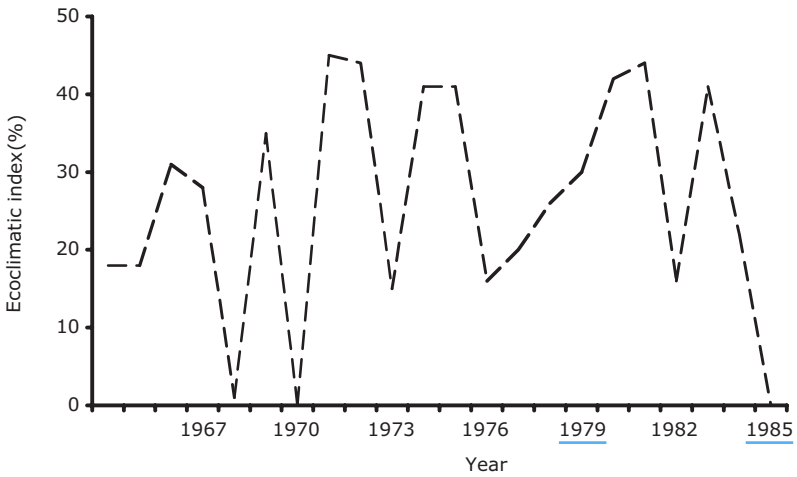

Fig. 6. Variation in ecoclimatic index, EI, for monarchs in south-east Queensland across years 1965–85 based on climatic data for Amberley (27°36′S, 152°42′E).

Host quality may also impact on herbivore abundance and impact. This may be a consequence of the limited gene pool of plants available, or to unique genotypes being present as a result of breeding or introductions from multiple sources (e.g. *Lantana camara* and mesquite species). Host quality may also be influenced by factors such as soil attributes, climate, plant density and the presence of other herbivores and pathogens. One poorly understood aspect of plant quality is the possible role of symbionts, such as the influence of nitrogen-fixing rhizobia on plant nitrogen composition (van Klinken 1999). Symbiont relationships are often modified in the native range (Wolfe & Klironomos 2004).

Habitat

Potential direct effects of habitat on the agent may need to be considered, particularly where the target weed populations occur in habitats that differ from those in the agents native range. For example, the most serious *Mimosa pigra* L. infestations in Australia are inundated for long periods of the year, which is different from its native range. Potential agents that pupate in the soil will therefore need specific strategies to overcome this.

Ultimately weed biological control is about plant population dynamics. Understanding why a plant is abundant is going

to be central to its control. Although not the focus of this contribution building a plant population model should be a major part of any weed biological control program. As with insects one could take a CLIMEX approach and at least infer where the weed species is likely to do well with respect to climate. Overlapping the agent and weed model can help one infer where the impact may be expected to be greatest. However, predicting such impacts will require better understanding of how herbivory may limit plant dynamics (Raghu *et al*. 2006).

Natural enemies

A weed biocontrol agent will be exposed to different suites of natural enemies in its native range to in its introduced range. Often populations in the native range may be under suppression by specialist natural enemies, as can be determined via exclusion experiments, either with cages or judicious use of insecticides. In this case, we would expect populations to reach high levels in the release environment, all else being equal. This is particularly true if the agent belongs to a taxon that is poorly represented in the introduced range, such as hispine beetles in Australia (McFadyen & Spafford-Jacob 2004), or are biologically unique.

Likely exposure to generalist natural enemies is probably more difficult to predict, as exposures can be quite different between natural and introduced ranges. For example, the ant fauna is particularly diverse and ubiquitous in Australia when compared with other continents (Naumann 1991). Some indication of susceptibility can be gained from knowing the natural enemy load on similar organisms within the target environment. For example, the diverse parasitoid fauna on *Evippe* sp. #1 (Gelechiidae), a leaf-tying moth on mesquite introduced into Australia from Argentina, could be predicted as Australia has a diverse native fauna of semi-concealed leaf-feeding Lepidoptera, and therefore almost certainly a diverse parasitoid fauna (van Klinken & Burwell 2005). Similarly, *Penthobruchus germaini* (Pic), a seed-feeding beetle released against *Parkinsonia aculeata* L. in Australia, was suppressed by a trichogramattid egg parasitoid (van Klinken 2005). This suggests that further seed-feeding agents targeting rangeland shrubs need to have demonstrated mechanisms for avoiding this widespread and abundant parasitoid.

In many cases it is possible to identify at least some of the natural enemies that a potential agent will be susceptible to within its native range (Edwards *et al*. 1996); the challenge is to predict the level of parasitism and whether it will be sufficient to limit impact on the target weed (van Klinken & Burwell 2005). The natural enemy load on an agent can be very diverse, but not necessarily result in significant overall mortality (van Klinken & Burwell 2005). Alternatively, agents can be effective despite relatively high and prolonged levels of parasitism (Bess & Haramoto 1972).

Natural enemies can have a big impact on new introductions. There are many anecdotal examples where authors have claimed the introduced agent was ineffective due to local natural enemies (Goeden & Louda 1976; Cullen 1995). Although most of these claims are unsubstantiated with experimental evidence and seem to be convenient *post hoc* explanations for apparent failure, there are well-documented exceptions (Briese 1986). A trial following the fate of eggs and larvae of a geometrid moth (*Anaitis efformata* Guenee) released in Australia against St John's Wort (*Hypericum perforatum* L.) showed that predation by generalist predators and egg parasitism were primary factors limiting agent populations there (Briese 1986). A national post-release evaluation of a seed-feeding beetle on *P. aculeata* L., and subsequent modelling, showed that egg parasitoids cause a substantial reduction in seed predation rates on *P. aculeata* L. in Australia (van Klinken 2005; R van Klinken unpubl. data 2006).

DISCUSSION

Population ecologists are generally interested in explaining the patterns of abundance and distribution of the species they study. Where a species is found and how many occur at any one time are not constant. Rather, abundance and distribution are dynamic, changing at varying rates over time and space (Hengeveld 1990). Many theories have been proposed to account for this variation, and these can be broadly divided into two groups: those that view climate, either directly or indirectly through its interactions with species-specific characters, as the major determining factor (Andrewartha & Birch 1954; Walter & Zalucki 1999); and those that view multi-species interactions such as competition and predation as being paramount (Pimm 1991). The debate among the various schools has engendered more heat than light. The approach of both tends to be descriptive; each attempts to account for patterns in data, either statistically or by using models derived from theory. Rarely does either school attempt to test predictions by direct experiment. Biological control programs offer that opportunity and continue to contribute to the development of ecological theory.

It is possible to make predictions of where a species may be found and in what relative abundance, and at least partially test them, and so shed some light on the influence of climate and other factors on species abundance and distribution. Any species that has a wide and variable distribution will suffice. Species that have been either accidentally or deliberately introduced to new geographical areas, and have established and spread, fit this description. Classic biological control programs move species into new areas all the time. We have used the monarch butterfly, to illustrate the approach and to briefly explore long-term changes in abundance at one location. We first described the effect of climate variables on the species' range in one geographical region (Australia). We then used that description to predict its abundance and distribution in other regions (North America). Concordance between the predicted and observed distributions can be used to indicate that climate may well account for the species range. Discrepancies indicate that other factors need to be included, or that our model is not appropriate.

The CLIMEX parameter set integrates data on species distribution into a single model that can be used to infer a species likely geographical distribution and, as we have outlined, changing abundance as well (Fig. 3). This approach may be used to generate a climate-driven null model for the abundance of a species at a site over time. The minimum data set required to use this bio-climatic approach to infer the temporal abundance of a species is the geographical distribution of that species, although additional information on relative abundance across the species range and seasonal variation in abundance will aid the process. Such information is more likely to be available for a species than are long-term measures of abundance (say 10–20 years of data!).

Models that enable one to infer likely species abundance based on climate are critical to testing effectiveness of management strategies such as area wide management and planting of transgenic crops (e.g. Carriere *et al*. 2003; Zalucki & Furlong 2005), as well as predicting temporal dynamics of introduced agents. Such a model could be used to not only select climatically suitable sites for release of agents, but also which season, and even which years might be better suited for release as well as 'predicting' expected dynamics post release. The latter can be particularly useful when trying to interpret why a species appears to be at low levels of abundance. Sites where a species has been introduced may on average be climatically suitable but the weather may be highly variable and the release may have been made during a drier or wetter than average series of years.

Historical climate data can be used to predict the expected range and variation in the temporal dynamic (seasonally and annually) of the phytophage, and therefore of likely impacts. For example, if the phytophages populations are expected to vary tremendously from year to year, will its cumulative effect still be expected to result in the desired weed impact? A wide range of scenarios are possible, depending in part on the synchronicity between plant and phytophage dynamics.

To make predictions of temporal dynamics before an agent is released will of course require better forecasts of climate! In that sense predictions may in fact remain a 'gazing into a crystal ball' exercise. Nevertheless, having such a climate-based model may enable researchers to confirm or eliminate climate as a likely cause of low abundance before clutching at other likely causes of failure, such as predation. Although we have shown that such models may be relatively simple to derive, the irony is that they need to be tested against independent data sets if they are to be used in pest management or biological control programs with any confidence. Such independent data may be the species geographical distribution not used in deriving the model, but more importantly long series abundance data for a site! The conundrum is that such data are less likely to be available unless collecting such data is made, as they should be, part and parcel of biological control programs.

The approach we have outlined is to some extent circumscribed by the package we have used. CLIMEX essentially proposes a species distribution is entirely determined by responses to moisture and temperature. It is possible to derive a model for a species population dynamics as driven by climate and other factors using say DYMEX as a modelling tool (Maywald *et al*. 1999). Such models may simply attempt to predict seasonal phenology based on the insects developmental biology (e.g. Mohandass & Zalucki 2004) or include a comprehensive description of what is known to impact on a species population dynamics (e.g. Yonow *et al*. 2004). The latter is unlikely to be possible for an agent selected for release. But the former is not difficult, particularly if the developmental biology has been derived before release or has been established during the breeding program for a species in quarantine or during the mass-rearing phase. In these situations it should not be difficult to derive the developmental zero, degree-day requirements, upper-temperature limit, etc. for each developmental stage; see Scott and Yeoh (1999) for a case study based on an accidentally introduced aphid. Alternatively, a simple phenology model can be very useful when interpreting field population abundance data (e.g. Malcolm *et al*. 1987; Zalucki & Rochester 2004). In particular, the absence of generations when predicted may indicate the presence of diapause or migration which may be critical to the success of an introduced agent.

Abundance of an introduced phytophagous insect will not only depend on the weather, but also the quality of the host plant as well as their own natural enemies (e.g. generalist predators, etc.). Only experimental manipulation of populations can reveal the relative contribution of such factors to reproduction and mortality. These essentially exclusion studies (e.g. Furlong *et al*. 2004a,b) can be undertaken in the home range and post release to identify not only what has happened to the agent but also the impact on the plant (Sheppard *et al*. 2001).

CONCLUSIONS

Predicting the distribution and abundance of a potential agent in a new environment tests our most fundamental understanding of ecology, and therefore is a daunting task. Absolute predictions are likely to remain elusive, even for the best-studied organisms. Predictions should, nonetheless, be of sufficient quality to help prioritise potential agents on the basis of likely abundance, and rule out at least some potential agents on the basis of climate and other factors. Predictions will have direct benefits to designing release strategies and for the design and interpretation of agent evaluation studies. Continued improvement of predictions is, however, contingent on the application, testing and refinement of existing theories within active biological control programs.

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REFERENCES

Adair RJ & Scott JK. 1997. Distribution, life history and host specificity of *Chrysolina picturata* and *Chrysolina* sp. B (Coleoptera: Chrysomelidae), two biological control agents for *Chrysanthemoides monilifera* (Compositae). *Bulletin of Entomological Research* **87**, 331–341.

Andrewartha A & Birch LC. 1954. *The Distribution and Abundance of Animals*. University of Chicago Press, Chicago, USA.

Barbosa P & Schultz JC, eds. 1987. *Insect Outbreaks*. Academic Press, New York, USA.

Bess HA & Haramoto FH. 1972. Biological control of pamakani, *Eupatorium adenophorum*, in Hawaii by a tephritid gall fly, *Procecidochares utilis* III. Status of the weed, fly and parasites of the fly in 1966–1971. *Proceedings of the Hawaiian Entomological Society* **21**, 165–178.

Blakley NR & Dingle H. 1978. Competition: butterflies eliminate milkweed bugs from a Caribbean island. *Oecologia* **37**, 133–136.

Briese DT. 1986. Factors affecting the establishment and survival of *Anaitis efformata* (Lepidoptera: Geometridae) introduced into Australia for the biological control of St. John's Wort, *Hypericum perforatum*. II. Field trials. *Journal of Applied Ecology* **23**, 821–839.

Buckley YM, Briese DT & Rees M. 2003. Demography and management of the invasive species *Hypericum perforatum*: 1. Using multi-level mixed effects models for characterising growth, survival and fecundity in a long-term dataset. *Journal of Applied Ecology* **40**, 481–493.

Buckley YM, Rees M, Paynter QP & Lonsdale M. 2004. Modelling integrated weed management of an invasive shrub in tropical Australia, *Mimosa pigra*. *Journal of Applied Ecology* **41**, 547–560.

Buckley YM, Rees M, Sheppard AW & Smyth MJ. 2005. Impact of biocontrol on the invasive plant *Echium plantagineum*: a coupled plant-herbivore model. *Journal of Applied Ecology* **42**, 70–79.

Busby JR. 1991. BIOCLIM – a bioclimate analysis and prediction system. *Plant Protection Quarterly* **6**, 8–9.

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.

CarriereY, Ellers-Kirk C, Sisterson M *et al.* 2003. Long-term regional suppression of pink bollworm by *Bacillus thuringiensis* cotton. *Proceedings of the National Academy of Science* **100**, 1519–1523.

Caughley G. 1976. Plant-Herbivore systems. In: *Theoretical Ecology: Principles and Applications* (ed. RM May), pp. 94–113. Blackwell Scientific Publications, Oxford, UK.

Clarke AR & Zalucki MP. 2004. Monarchs in Australia: on the winds of a storm? *Biological Invasions* **6**, 123–127.

Cullen JM. 1995. Predicting effectiveness: fact and fantasy. In: *Proceedings of the Eighth International Symposium on Biological Control of Weeds, 2–7 February 1992* (eds ES Delfosse & RR Scott), pp. 103–109. DSIR/CSIRO, Melbourne, Australia.

Dallwitz MJ & Higgins JP. 1978. *Users Guide to DEVAR: A Computer Program for Estimating Development Rate as a Function of Temperature*. CSIRO, Canberra, Australia.

Dallwitz R. 1984. The influence of constant and fluctuating temperatures on development rate and survival of pupae of the Australian sheep blowfly *Lucilia cuprina*. *Entomologia Experimentalis et Applicata* **36**, 89–95.

Dennill GB & Gordon AJ. 1990. Climate-related differences in the efficacy of the Australia gall wasp (Hymenoptera: Pteromalidae) released for control of *Acacia longifolia* in South Africa. *Environmental Entomology* **19**, 130–136.

Dingle H, Zalucki MP, Rochester WA & Armijo-Prewitt T. 2005. Distribution of the monarch butterfly, *Danaus plexippus* in western North America. *Biological Journal of the Linnean Society* **85**, 491–500.

Dodd AP. 1940. *The Biological Campaign Against Prickly-Pear*. Government Printer, Brisbane, Australia.

Edwards PB, Adair RJ & Holtkamp RH. 1996. Seedhead tephritids and their parasitoids – can predictions be made about likely parasitism of tephritids introduced into Australia for biological control of Asteraceae? In: *Proceedings of the Ninth International Symposium on Biological Control of Weeds, 19–26 January 1996* (eds VC Moran & JH Hoffmann), pp. 153–164. University of Cape Town, Cape Town, South Africa.

Furlong MJ, Shi Z-H, Liu Y-Q *et al.* 2004a. Experimental analysis of the influence of pest management practice on the efficacy of an endemic arthropod natural enemy complex of the diamondback moth. *Journal of Economic Entomology* **97**, 1814–1827.

Furlong MJ, Shi Z-H, Liu S-S & Zalucki MP. 2004b. Evaluation of the impact of natural enemies on *Plutella xylostella* L. (Lepidoptera: Yponomeutidae) populations on commercial *Brassica* farms. *Agricultural and Forest Entomology* **6**, 311–322.

Goeden RD & Louda SM. 1976. Biotic interference with insects imported for weed control. *Annual Review of Entomology* **20**, 325–342.

Goolsby J, van Klinken R & Palmer WA. 2006. Maximising the contribution of native-range studies towards the identification and prioritisation of weed biocontrol agents. *Australian Journal of Entomology* **45**, 276–286.

Gregg PC, Fitt GP, Zalucki MP & Murray DAH. 1995. Insect migration in an arid continent. II *Helicoverpa* in Eastern Australia. In: *Insect Migration: Tracking Resources Through Space and Time* (eds VA Drake & AG Gatehouse), pp. 151–172. Press Syndicate of University of Cambridge, Cambridge, UK.

Heard TA & Forno IW. 1996. Host selection and host range of the flower-feeding weevil, *Coelocephalapion pigrae*, a potential biological control agent of *Mimosa pigra*. *Biological Control* **6**, 83–95.

Hengeveld R. 1990. *Dynamic Biogeography*. Cambridge Studies in Ecology, Cambridge University Press, Cambridge, UK.

Hughes RD & Maywald GF. 1990. Forecasting the favourableness of the Australian environment for the Russian wheat aphid, *Diuraphis noxia* (Homoptera: Aphididae), and its potential impact on Australian wheat yields. *Bulletin of Entomological Research* **80**, 165–175.

Julien MH, Kerr JD & Chan RR. 1984. Biological control of weeds: an evaluation. *Protection Ecology* **7**, 3–25.

Julien MH, Skarratt B & Maywald GF. 1995. Potential geographic distribution of alligator weed and its biological control by *Agasicles hygrophila*. *Journal of Aquatic Plant Management* **33**, 55–60.

Kleinjan CA & Scott JK. 1996. Selection of *Cassida* spp. from southern Africa for the biological control of *Chrysanthemoides monilifera* in Australia. *Annals of Applied Biology* **128**, 373–385.

Krebs CJ. 2001. *Ecology.* Benjamin Cummings, San Francisco, USA.

Kriticos DJ. 2003. The roles of ecological models in evaluating weed biological control agents and projects. In: *Improving the Selection, Testing and Evaluation of Weed Biological Control Agents* (eds H Spafford-Jacob & DT Briese), pp. 69–74. Cooperative Research Centre for Australian Weed Management, Adelaide, Australia.

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

Kriticos DJ, Brown JR, Radford ID & Nicholas M. 1999. Plant population ecology and biological control: *Acacia nilotica* as a case study. *Biological Control* **16**, 230–239.

Kriticos DJ, Sutherst RW, Brown JR, Adkins SA & Maywald GF. 2003. Climate change and the potential distribution of an invasive alien plant: *Acacia nilotica* ssp. *indica* in Australia. *Journal of Applied Ecology* **40**, 111–124.

Liu S-S, Chen F-Z & Zalucki MP. 2002. Development and survival of the diamondback moth, *Plutella xylostella* (Lepidoptera: Plutellidae), at constant and alternating temperatures. *Environmental Entomology* **31**, 1–12.

Malcolm SB, Cockrell BJ & Brower LP. 1987. Monarch butterfly voltinism: effects of temperature constraints at different latitudes. *Oikos* **48**, 77–82.

Matsuki M, Kay M, Serin J, Floyd R & Scott JK. 2001. Potential risk of accidental introduction of Asian gypsy moth (*Lymantria dispar*) to Australasia: effects of climatic conditions and suitability of native plants. *Agriculture and Forestry Entomology* **3**, 305–320.

Matthews M. 1999. *Heliothine Moths of Australia*. Monographs on Australian Lepidoptera Vol. 7. CSIRO, Collingwood, Australia.

Maywald GF & Sutherst RW. 1991. *Users Guide to CLIMEX a Computer Program for Comparing Climates in Ecology*, 2nd edn. CSIRO Australia, Division of Entomology Report No. 48. CSIRO, Canberra, Australia.

Maywald GF, Sutherst RW & Zalucki MP. 1999. *DYMEX Professional: Modelling Natural Systems, CD-ROM.* CSIRO Publishing, Melbourne, Australia.

McClay AS. 1996. Biological control in a cold climate: temperature responses and climatic adaptation of weed biocontrol agents. In: *Proceedings of the IX International Symposium on Biological Control of Weeds* (eds VC Moran & JH Hoffmann), pp. 368–377. University of Cape Town, Cape Town, South Africa.

McFadyen REC. 1998. Biological control of weeds. *Annual Review of Entomology* **43**, 369–393.

McFadyen REC & Skarratt B. 1996. Potential distribution of *Chromolaena odorata* (siam weed) in Australia and Oceania. *Agriculture Ecosystems and Environment* **59**, 89–96.

McFadyen REC & Spafford-Jacob H. 2004. Insects for the biocontrol of weeds: predicting parasitism levels in the new country. In: *The Eleventh International Symposium on Biological Control of Weeds* (eds JM Cullen, DT Briese, DJ Kriticos, WM Lonsdale, L Morin & JK Scott), pp. 135–140. CSIRO Entomology, Canberra, Australia.

Mohandass S & Zalucki MP. 2004. DBM Development: are we measuring the right temperatures? In: *The Management of Diamondback Moth and Other Crucifer Pests: Proceedings of the Fourth International Workshop* (eds NM Endersby & PM Ridlands), pp. 117–122. The Regional Institute, Gosford, Australia.

Myers JH. 1987. Population outbreaks of introduced insects: lessons from the biological control of weeds. In: *Insect Outbreaks* (eds P Barbosa & J Schultz), pp. 173–193. Academic Press, New York, USA.

Naumann I. 1991. Hymenoptera (wasps, bees, ants, sawflies). In: *The Insects of Australia: A Textbook for Student and Research Workers*, pp. 916–1000. Melbourne University Press, Melbourne, Australia.

Nicholls AO. 1989. How to make biological surveys go further with generalised linear models. *Biological Conservation* **50**, 51–75.

Peterson AT. 2003. Predicting the geography of species invasion via ecological niche modeling. *Quarterly Review of Biology* **78**, 419–433.

Pimm S. 1991. *The Balance of Nature?* University of Chicago Press, Chicago, USA.

Raghu S, Wilson JR & Dhileepan K. 2006. Refining the process of agent selection through understanding plant demography and plant response to herbivory. *Australian Journal of Entomology* **45**, 308–316.

Robertson MP, Peter CI, Villet MH & Ripley BS. 2003. Comparing models for predicting species' potential distributions: a case study using correlative and mechanistic predictive modelling techniques. *Ecological Modelling* **164**, 153–167.

Rogers D. 1979. Tsetse population dynamics and distribution: a new analytical approach. *Journal of Animal Ecology* **48**, 825–849.

Room PM. 1986. *Salvinia molesta* – a floating weed and its biological control. In: *The Ecology of Exotic Animals and Plants* (ed. RL Kitching), pp. 164–186. John Wiley and Sons, Brisbane, Australia.

Samways MJ, 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.

Scott JK. 1992. Biology and climatic requirements of *Perapion antiquum* (Coleoptera: Apionidae) in southern Africa: implications for the biological control of *Emex* species in Australia. *Bulletin of Entomological Research* **82**, 399–406.

Scott JK & Yeoh PB. 1999. Bionomics and the predicted distribution of the aphid *Brachycaudus rumexicolens* (Hemiptera: Aphididae). *Bulletin of Entomological Research* **89**, 97–106.

Sheppard AW, Smyth MJ & Swirepik A. 2001. The impact of a root-crown weevil and pasture competition on the winter annual *Echium plantaginem*. *Journal of Applied Ecology* **38**, 291–300.

Spradbery JP & Maywald GF. 1992. The distribution of the European or German Wasp, *Vespula germanica* (F.) (Hymenoptera: Vespidae), in Australia: past, present and future. *Australian Journal of Zoology* **40**, 495–510.

Steinbauer MJ, Yonow T, Reid IA & Cant R. 2002. Ecological biogeography of species of *Gelonus*, *Acantholybas* and *Amorbus* in Australia. *Austral Ecology* **27**, 1–25.

Sutherst RW. 2003. Prediction of species geographical ranges [Guest editorial]. *Journal of Biogeography* **30**, 1–12.

Sutherst RW. 2004. Prediction of species' geographical ranges. A critical comment on M.J. Samways, R. Osburn, H. Hastings and V. Hattingh (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. *Journal of Biogeography* **30**, 805–816.

Sutherst RW & Maywald GF. 1985. A computerized system for matching climates in ecology. *Agriculture, Ecosystems and Environment* **13**, 281–300.

Sutherst RW & Maywald GF. 2004. *CLIMEX Version 3, Users Guide.* Hearne Scientific Software, Melbourne, Australia.

Sutherst RW & Maywald GF. 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, Spradbery JP & Maywald GF. 1989. The potential geographic distribution of the old world screw worm fly, *Chysomya bezziana*. *Medical and Veterinary Entomology* **3**, 273–280.

Sutherst RW, Floyd RB & Maywald GF. 1995. The potential geographic distribution of the cane toad, *Bufo marinus* L. in Australia. *Conservation Biology* **9**, 294–299.

Sutherst RW, Maywald GF, Yonow T & Stevens PM. 1999. *CLIMEX: Predicting the Effects of Climate on Plants and Animals. Users Guide and CD-ROM*. CSIRO Publishing, Melbourne, Australia.

Sutherst RW, Collyer BS & Yonow T. 2000. The vulnerability of Australian horticulture to the Queensland fruit fly, *Bactrocera* (Dacus) *tryoni*, under climate change. *Australian Journal of Agricultural Research* **51**, 467–480.

van Klinken RD. 1999. Developmental host-specificity of *Mozena obtusa* (Heteroptera: Coreidae), a potential biocontrol agent for mesquite (*Prosopis* species). *Biological Control* **16**, 283–290.

van Klinken RD. 2005. Total annual seed loss on a perennial legume through predation by insects: the importance of within-season seed and seed-feeder dynamics. *Austral Ecology* **30**, 414–425.

van Klinken RD & Burwell C. 2005. Evidence from a gelechiid leaf-tier on mesquite (Mimosaceae: *Prosopis*) that semi-concealed Lepidopteran biological control agents may not be at risk from parasitism in Australian rangelands. *Biological Control* **32**, 121–129.

van Klinken RD & Raghu S. 2006. A scientific approach to agent selection. *Australian Journal of Entomology* **45**, 253–258.

van Klinken RD, Fichera G, Parr R *et al.* 2002. Challenges facing the successful management of widely distributed weeds: biological control of mesquite (*Prosopis* species). In: *Thirteenth Australian Weeds Conference: Papers and Proceedings* (eds H Spafford-Jacobs, J Dodd & JH Moore), pp. 370–374. Plant Protection Society of Western Australia, Perth, Australia.

van Klinken RD, Fichera G & Cordo H. 2003. Targeting biological control across diverse landscapes: the release, establishment and early success of two insects on mesquite (*Prosopis*) in rangeland Australia. *Biological Control* **26**, 8–20.

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.

Walter H & Lieth H. 1960. *Klimadiagramm Weltatlas* 1. Lieferung mit 12 Karten. Fischer Verlag, Jena, Germany.

Walter G & Zalucki MP. 1999. Rare butterflies and theories of evolution and ecology. In: *Biology of Australian Butterflies* (eds RL Kitching, E Scheermeyer, RE Jones & NE Pierce), pp. 349–368. CSIRO Publishing, Melbourne, Australia.

Wapshere AJ. 1974. The regions of infestation of wool by Noogoora burr (*Xanthium strumarium*), their climates and the biological control of the weed. *Australian Journal of Agricultural Research* **25**, 775–781.

Wapshere AJ. 1983. Discovery and testing of a climatically adapted strain of *Longitarsus jacobaeae* (Coleoptera: Chrysomelidae) for Australia. *Entomophaga* **28**, 27–32.

Wapshere AJ. 1993. Climate matching and the prospects for biological control of weeds: the contrasting examples of agents for *Solanum elaegnifolium* and *Heliotropium amplexicaule*. In: *Pest Control and Sustainable Agriculture* (eds SA Corey, DJ Dall & WM Milne), pp. 198–200. CSIRO, Melbourne, Australia.

Wharton TN & Kriticos DJ. 2004. The fundamental and realized niche of the Monterey Pine aphid, *Essigella californica* (Essig) (Hemiptera: Aphididae): implications for managing softwood plantations in Australia. *Diversity and Distributions* **10**, 253–262.

Wolfe BE & Klironomos JN. 2004. Breaking new ground: soil communities and exotic plant invasion. *Bioscience* **55**, 477–487.

Yonow T & Sutherst RW. 1998. The geographical distribution of Queensland fruit fly, *Bactrocera (Dacus) tryoni*, in relation to climate. *Australian Journal of Agricultural Research* **49**, 935–953.

Yonow T, Zalucki MP, Sutherst RW *et al.* 2004. Modelling the population dynamics of the Queensland fruit fly, *Bactrocera (Dacus) tryoni*: a cohort-based approach incorporating the effects of weather. *Ecological Modelling* **173**, 9–30.

Zalucki MP. 1982. Temperature and rate of development in two species of *Danaus*, *D. plexippus* and *D. chrysippus*. *Journal of the Australian Entomological Society* **21**, 241–246.

Zalucki MP & Clarke AR. 2004. Monarchs across the pacific: the Columbus hypothesis revisited. *Biological Journal of the Linnean Society* **81**, 111–121.

Zalucki MP & Furlong MJ. 2005. Forecasting *Helicoverpa* populations in Australia: a comparison of regression based models and a bioclimatic modelling based approach. *Insect Science* **12**, 45–56.

Zalucki MP & Kitching RL. 1984. The dynamics of adult *Danaus plexippus* L. (Danaidae) within patches of its food plant, *Asclepias* spp. *Journal of the Lepidopterists' Society* **38**, 209–219.

Zalucki MP & Rochester WA. 1999. Estimating the effect of climate on the distribution & abundance of the monarch butterfly, *Danaus plexippus* (L.): a tale of two continents. In: *The 1997 North American Conference on the Monarch Butterfly* (eds J Hoth, L Merino, K Oberhauser, I Pisantry, S Price & T Wilkinson), pp. 150–163. Commission for Environmental Co-operation, Montreal, Canada.

Zalucki MP & Rochester WA. 2004. Spatial and temporal population dynamics of monarchs down-under: lessons for North America. In: *The Monarch Butterfly: Biology and Conservation* (eds K Oberhauser & M Solensky), pp. 219–228. Cornell University Press, Ithaca, USA.

Zalucki MP, Daglish G, Firempong S & Twine PH. 1986. The biology and ecology of *Heliothis armigera* (Hübner) and *H. punctigera* Wallengren (Lepidoptera; Noctuidae) in Australia. What do we know? *Australian Journal of Zoology* **34**, 779–814.

Zalucki MP, Hughes JM, Arthur JM & Carter PA. 1993. Temporal variation at four loci in a continuously breeding population of *Danaus plexippus*. *Heredity* **70**, 205–213.

Zalucki MP, Gregg PC, Fitt GP, Murray DAH, Twine PH & Jones C. 1994. Ecology of *Helicoverpa armigera* (Hübner) and *H. punctigera* (Wallengren) in the inland areas of eastern Australia: larval sampling and host plant relationships during winter/spring. *Australian Journal of Zoology* **42**, 329–346.

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