Climate change and voltinism in Californian insect pest species: sensitivity to location, scenario and climate model choice

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Abstract

Experimental studies of the impact of climatic change are hampered by their inability to consider multiple climate change scenarios and indeed often consider no more than simple climate *sensitivity* such as a uniform increase in temperature. Modelling efforts offer the ability to consider a much wider range of realistic climate projections and are therefore useful, in particular, for estimating the sensitivity of impact predictions to differences in geographical location, and choice of climate change scenario and climate model projections. In this study, we used well-established degree-day models to predict the voltinism of 13 agronomically important pests in California, USA. We ran these models using the projections from three Atmosphere–Ocean Coupled Global Circulation Models (AOCGCMs or GCMs), in conjunction with the SRES scenarios. We ran these for two locations representing northern and southern California. We did this for both the 2050s and 2090s. We used ANOVA to partition the variation in the resulting voltinism among time period, climate change scenario, GCM and geographical location. For these 13 pest species, the choice of climate model explained an average of 42% of the total variation in voltinism, far more than did geographical location (33%), time period (17%) or scenario (1%). The remaining 7% of the variation was explained by various interactions, of which the location by GCM interaction was the strongest (5%). Regardless of these sources of uncertainty, a robust conclusion from our work is that all 13 pest species are likely to experience increases in the number of generations that they complete each year. Such increased voltinism is likely to have significant consequences for crop protection and production.

Keywords: agricultural pests, climate change, degree-days, global warming, voltinism

Received 22 August 2011; revised version received 3 May 2012 and accepted 13 May 2012

Introduction

How climatic change will affect agricultural systems is clearly a question of concern (Olfert *et al.*, 2011), directly applicable to important global issues such as food security (Gregory *et al.*, 2009). An understanding of the potential impacts of climatic change on agricultural pests is necessary if we want to be able to predict the response of agricultural systems to that change. Temperature changes can directly affect insect development, survival, range, population density and voltinism (Bale *et al.*, 2002). Yet, studies investigating the response of agricultural pests to climate change are relatively uncommon (Mika *et al.*, 2008). If progress is to be made in developing strategies to adapt agricultural systems to the impacts of climatic change, such studies are critically important. This is particularly true

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in areas such as California, a state that is economically dependent on its agricultural industry, and encompasses several climatic zones (Hayhoe *et al.*, 2004).

Model-based studies are a valuable method for predicting the impacts of climatic change on insect pests (Jönsson *et al.*, 2009; Olfert *et al.*, 2011). While there are various ways to represent the climatic changes in modelling studies, more sophisticated treatments use climate projections derived from global circulation models (GCMs, Mika *et al.*, 2008). Numerous researchers have relied on this approach to predict biological impacts. For example, GCM-derived projections have been utilized to predict: the future distribution and abundance of crop pests (Olfert *et al.*, 2011), butterfly extinction rates (Beaumont & Hughes, 2002) and voltinism of forestry pests (Jönsson *et al.*, 2009). Projections from GCMs have also been used to estimate the impacts of climatic change on water resources (Buytaert *et al.*, 2009), to evaluate conservation policies (Harrison *et al.*, 2006) and to assess the risk of invasive species (Mika & Newman, 2010; Mika *et al.*, 2008).

For model-based impact studies such as these, it is important that sources of uncertainty are identified

and that we emphasize those results that are robust to these sources of uncertainty. In climate projections, there are three main sources of uncertainty: (i) the internal variability in the climate system, which arises from fluctuations not caused by radiative forcing; (ii) model uncertainty, which is a consequence of the different assumptions and simplifications used in different climate models; and (iii) scenario uncertainty, resulting from uncertainty about future greenhouse gas emissions. Hawkins & Sutton (2009) showed that for predictions of surface temperature, the contribution of model uncertainty to total uncertainty in projections is relatively constant across all timescales. Scenario uncertainty is more important than model uncertainty for projections >50 years in the future, and less important than model uncertainty for more proximate projections. Internal variability is more important than either model or scenario uncertainty for projections <20 years in the future, but for longer time horizons, internal variability is relatively unimportant. As much of the modelling work on the biological impacts of climatic change considers periods from 60 to 100 years in the future, researchers using GCM-derived climate projections need to mainly worry about uncertainties (ii) and (iii). That is, we must decide which climate model(s) and which scenario(s) to use. Researchers sometimes confound these two sources of uncertainty by comparing different model-scenario combinations without holding either the scenario, or the model, constant (e.g. Carroll *et al.*, 2010). The importance of scenario choice in impact studies has been discussed extensively by others (Beaumont *et al.*, 2007); indeed, this is often considered to be the most significant source of uncertainty in the use of climate model outputs (Quiggin, 2008).

The potential of different climate models to influence predictions has received less attention than has the issue of scenario choice. As of the fourth assessment report of the Inter-governmental Panel on Climate Change (Randall *et al.*, 2007), there were 23 different atmosphere–ocean coupled GCMs, developed by 18 climate modelling centres globally. Each model has both strengths and weaknesses, with no single model considered 'best' overall at projecting the climate (Bader *et al.*, 2008; Meehl *et al.*, 2007). Although all models project an increase in global mean surface air temperatures over the next century (Meehl *et al.*, 2007), this general consensus can be coarse from an ecological perspective. Variation between different climate models can certainly influence biological results, and predicting biological impacts based on projections from only one GCM may be misleading (Beaumont *et al.*, 2008; Newman, 2006). As there is no 'best' model, researchers

need to consider a number of models to reach robust conclusions, or at least to characterize the model dependence of their predictions (Parker, 2006).

The use of multiple GCMs in impact studies is only recently becoming common practice (Buisson *et al.*, 2010), likely a consequence of the increasing number of studies that are noting discrepancies in predicted impacts as a result of model choice. For example, Olfert *et al.* (2011) noted varying responses to model inputs for the three GCMs used in their study of the crop pest *Melanoplus sanguinipes*, and in a study by Kriticos *et al.* (2009), the variability in results caused by different GCMs was as great as the variability caused by different scenarios. Mika *et al.* (2008) found that GCM choice could result in prediction of areas at risk for *Contarinia nasturtii* that diverged not just in magnitude but also in direction of change; see also Mika & Newman (2010). Results such as these have worrying implications for impact research and emphasize the need for studies that investigate model dependency of projected biological impacts.

Here, we used degree-day models to predict the number of generations per year (voltinism) of 13 pest species of economic importance in California, using temperature projections from each combination of three GCMs, three scenarios, three time periods and two locations (hereafter, referred to as 'sources of uncertainty'). We expected that different emissions scenarios would produce different predictions of impacts, particularly for the later time period. Similarly, we expected large differences in the predictions for different geographical locations, particularly later in the century. We did not think that model choice would be as important as these other sources of uncertainty. Degree-days are a measure of physiological time, or the amount of heat needed for an organism to develop. Degree-day models are commonly used in integrative pest management, as they yield a significant amount of information on insect development. As these models draw on daily minimum and maximum temperatures as inputs, they lend themselves particularly well to studies concerned with predicting the impacts of climatic change.

Material and methods

Pest degree-day models

We used degree-day models for 13 different agricultural pest species of economic importance in California (Table 1). We used the models recommended by the University of California's Cooperative Extension's Integrated Pest Management Program (UCIPM; http://ucipm.ucdavis.edu/). For all pests except the beet armyworm, we used the single sine and the horizontal cut-off setting. For the beet armyworm, we used

Table 1 Phenology and host crop data for the 13 agricultural pest species investigated

Organism	Generation parameters	Generation time DD (°F)/LDT/UDT (°F)	Agricultural host
Beet Armyworm (*Spodoptera exigua*)	Egg to Adult	882/54/NA (Hogg & Gutierrez, 1980)	Cotton (*Gossypium hirsutum*)
California Red Scale (*Aonidiella aurantii*)	Crawler to Crawler	1199/53/NA (Bimboni, 1970)	Grapefruit (*Citrus × paradisi*)
Codling Moth (*Cydia pomonella*)	Egg to Egg	1118/50/88 (Ohlendorf, 1999)	Apple/Pear (*Malus domestica / Pyrus communis*)
Elm Leaf Beetle (*Pyrrhalta (Xanthogaleruca) luteola*)	Egg to Egg	1206/52/NA (Dahlsten et al., 1993)	English Elms (*Ulmus procera*)
Lygus Bug (*Lygus hesperus*)	Egg to Egg	799/54/NA (Pickel et al., 1990)	Strawberries (*Fragaria sp.*)
Navel Orangeworm (*Amyelois transitella*)	Adult to Adult	1092/55/94 (Sanderson et al., 1989)	Mummy Almonds (*Prunus dulcis*)
Omnivorous Leafroller (*Platynota stultana*)	Egg to Adult	1168.2/48/87 (Kido et al., 1981)	Grapes (*Vitis vinifera*)
Orange Tortrix (*Argyrotaenia citrana*)	Adult to Adult	1636/43/78 (Bettiga et al., 1992)	Grapes (*Vitis vinifera*)
Oriental Fruit Moth (*Grapholita molesta*)	Egg to Egg	963/45/90 (Croft et al., 1980)	Peaches (*Prunus persica*)
Peach Twig Borer (*Anarsia lineatella*)	Adult to Adult	1060/50/88 (Rice et al., 1982a)	Almonds (*Prunus dulcis*)
Pink Bollworm (*Pectinophora gossypiella*)	Adult to Adult	885/57/91 (Beasley & Adams, 1996)	Cotton (*Gossypium hirsutum*)
San Jose Scale (*Quadraspidiotus perniciosus*)	n/a	1050/51/90 (Rice et al., 1982b)	Stonefruits/Almond (*Prunus sp.*)/(*Prunus dulcis*)
Tomato Fruitworm (*Helicoverpa (Heliothis) zea*)	Adult to Adult	872.8/55/92 (Hartstack et al., 1976)	Cotton (*Gossypium hirsutum*)

LDT = lower developmental threshold, UDT = upper developmental threshold. Note, several species do not have an UDT.

the double sine and horizontal cut-off setting. In each case, these were the default settings recommended by the UCIPM. These are working models with at least enough predictive power to be considered useful for actual management applications. There is considerable scope for tuning these models to account for specific genotypes, locations, microclimates, photoperiods, host plants and host-plant parts (see Scriber, 2010; and references therein). For the purposes of this study, we ignore these biological details. Uncertainty in the choice of biological model can be nontrivial (Thuiller, 2004), and it would be interesting to know how the magnitude of this source of uncertainty scales with those sources we consider in this article. Nevertheless, such quantification was beyond the scope of this study.

Degree-day models sometimes specify a calendar date after which time degree-days start accumulating, and/or a date after which degree-days stop accumulating. The UCIPM specified start dates for only three species and did not specify end dates for any of the 13 species. One impact of climatic change for any given location may be that the growing season (i.e. the presence of the host plants) starts earlier and/or ends later (see Appendix A, Supplemental Information). Without allowing flexibility for the start and end of degree-day accumulation, such impacts would be missed in a modelling exercise like this one. We therefore ran all the degree-day models on a calendar year basis. For

the three with specified start dates, the results of the two approaches differed by <10% (results not shown).

Climate change projections

Projections were downloaded from the Program for Climate Model Diagnosis and Intercomparison Working Group on Coupled Models CMIP3 multi-model data set (http://esg.llnl.gov:8080/index.jsp) as daily minimum and maximum temperature values for two locations, hereafter referred to as 'northern' and 'southern' (Fig. 1), for each of the A1B, A2 and B1 scenarios from the Special Report on Emissions Scenarios (Nakicenovic et al., 2000) for three GCMs. The three GCMs we used were the Canadian Centre for Climate Modelling and Analysis model CGC M3.1; the Australian Commonwealth Scientific and Industrial Research Organization model CSIRO Mk3.5 and the US National Oceanic and Atmospheric Administration's Geophysical Fluid Dynamics Laboratory model GFDL CM2.1. All projections were obtained for a 30 year baseline period (1961–1990), the 2050s (2046–2065) and the 2090s (2081–2100). Historical data for the baseline period were also obtained for the northern and southern California locations to provide a reference.

The A2, A1B and B1 scenarios are sometimes referred to as 'high', 'medium' and 'low' emissions scenarios, respectively

Fig. 1 Locations of the 'northern' and 'southern' locations. These locations represent approximately 4500 km². We extracted the daily minimum and daily maximum temperatures for each location from the relevant grid cell from each model. Northern location: CGC M3.1 = 38.97,−123.75; CSIRO Mk3.5 = 40.1,−121.88; GFDL CM2.1 = 39, −121.25. Southern location: CGC M3.1 = 35.26, −120; CSIRO Mk3.5 = 34.51,-118.12; GFDL CM2.1 = 35, −118.75. Note, the three models operate on different spatial scales; therefore the location of the centre of the grid cell that contains each location will differ between the models, but for each model, the locations are present in one, and only one, grid cell (i.e. our locations do not span grid cells in any of the three climate models).

(Meehl *et al.*, 2007). The A2 scenario depicts a future with slow economic growth and technological advancement, and high human population growth. The A1B scenario depicts a future of rapid economic growth and introduction of new and efficient technology – reliant on a balance of fossil and nonfossil energy sources – with moderate human population growth. The B1 scenario depicts a future with the same trend of moderate population growth as A1B, but with greater emphasis on environmental sustainability (Nakicenovic *et al.*, 2000).

Despite their large spatial scale, GCM projections are preferable to Regional Climate Model (RCM) output, or to statistically downscaled projections for the following reasons. First, it is rarely the case that there are multiple RCMs covering the same geographical area, so it would be difficult to assess the uncertainty due to climate model choice if we used RCM output. Second, despite their smaller spatial scale, RCMs are not necessarily more accurate than GCMs and can actually be less accurate (see Bader *et al.*, 2008, page 32 for further discussion). Like RCM results, statistically downscaled results are rarely readily available from multiple GCMs for the same locations, scenarios and time slices. So again, it would be difficult to conduct an assessment of model dependence. Also, like RCMs, the principle advantage to using downscaled results is for the use of precipitation projections, less so for temperature projections. As degree-day models only use daily minimum

and maximum temperatures, there are fewer advantages of using a downscaled approach.

Predicted impact of climatic change and variance partitioning

Projected daily minimum and maximum temperatures for each of the GCM–scenario–location–time combinations (hereafter referred to simply as 'projected futures') were averaged over each time period, such that for each time period there was only one minimum and maximum temperature for each day of a standard calendar year (Luedeling *et al.*, 2011 used the same logic in their recent, related work). We then ran degree-day models for each pest using temperatures from each projected future. For each case, the predicted number of generations per year was calculated by dividing the total number of accumulated degree-days generated by the degree-day model, by the number of degree-days required for the pest in question to complete one generation (Table 1).

We used analysis of variance as a tool to partition the variation in the predicted number of generations per year for each pest. We divided the sums of squares of each term by the total sum of squares to determine the percentage of the variation explained by each of the sources of uncertainty: model, scenario, time period, location and their interactions. Note that we are not using ANOVA to make statistical inferences; these models are deterministic and hence such inferences are not required.

Results

Climate change projections

Comparison of the minimum and maximum daily temperatures projected by each GCM–scenario–time–location combination revealed that the temperatures projected by each of the three GCMs were noticeably different, irrespective of the other factors. The GFDL model tended to projected cooler daily minimum and maximum temperatures, whereas the CSIRO model tended to project warmer minimum daily temperatures, particularly for the southern location (Fig. 2).

Partitioned variation

The results of the variance partitioning analysis followed the same trend across the entire range of pests investigated, in the order (from the source of uncertainty that explained the most variance in the results to the least) of climate model >location >time >location by climate model interaction >scenario. These sources explained on average 42%, 33%, 17%, 5% and 1% of the variation in the predicted number of generations per year of the 13 insect pests, respectively, with the remaining interaction terms explaining a combined 1.5% (Table 2). These percentages were similar across the 13 pest species (Fig. 3), although some discrepancies between organisms did exist (Fig. 4).
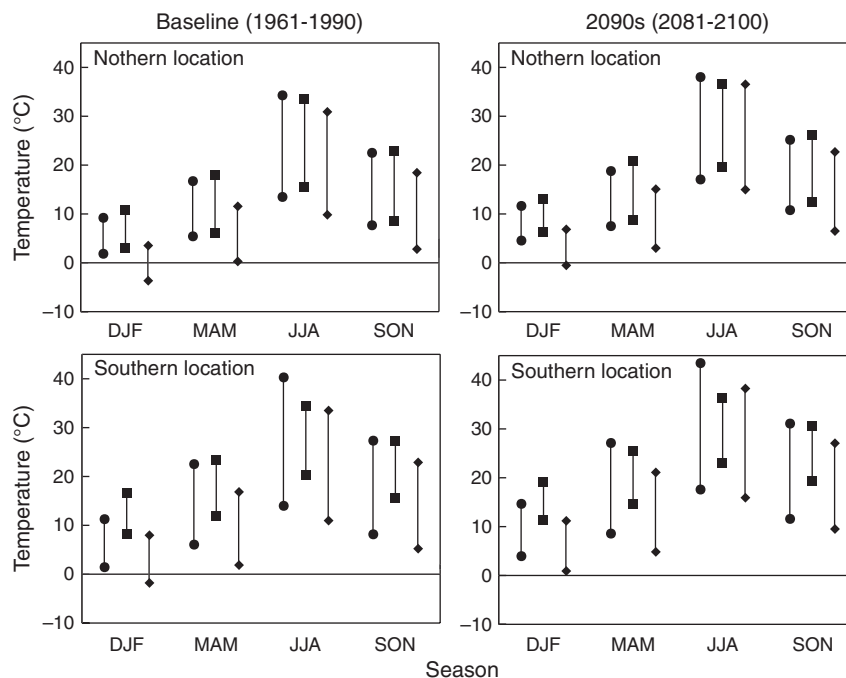
Fig. 2 Comparison of the minimum and maximum daily temperature projections across GCMs. The circle symbols represent projections from the Canadian climate model (CGCM3.1); the square symbols represent projections from the Australian climate model (CSIRO Mk3.5); and the diamond symbols denote projections from the US climate model (GFDL CM2.1). DJF = December, January, February (winter); MAM = March, April, May (spring); JJA = June, July, August (summer) and SON = September, October, November (autumn).

Table 2 Descriptive statistics of the variation in predicted voltinism explained by various sources of uncertainty, across 13 agricultural pest species in California, USA. 'Location: Model' refers to the interaction of geographical location and the climate model source used for the climate data

	Variance in voltinism (%)			
	Mean	Minimum	Maximum	Range
Model	42.19	37.21	53.16	15.95
Location	33.20	27.70	36.10	8.40
Time	17.15	12.83	20.46	7.63
Location:Model	4.93	4.10	7.53	3.43
Scenario	1.03	0.61	1.31	0.70
Other	1.51	0.81	2.70	1.89

Predicted response to climatic change

Although the predicted number of degree-days accumulated per year increased for all species and was greater in the south than the north, and greater in the later time period, these increases do not necessarily result in complete additional generations. Figure 4 shows the number of generations above those produced during the baseline period (averaged across all the scenarios as these produced little variation in the

degree of voltinism). We can see that for the 2050s in the northern location, none of the species increase by a complete generation under all of the three GCM projections. In the southern location, the only robust (to the choice of climate model) predictions of an extra generation were for the beet army-worm, the lygus bug and the oriental fruit moth. As we move further towards the end of the century, where warming becomes more significant, we see stronger indications of an additional generation. In the northern location, those indications are still mixed. The same three species that robustly increased by a complete generation in the south in the 2050s do so in the north by the 2090s. Seven other species are predicted to increase by a complete generation under projections from two of the climate models, but not under all three (i.e. that prediction is model dependent). In the south, however, the results are considerably more clear-cut. With the exception of the orange tortrix, the remaining 12 species all increase by at least a full generation per year under all three models, and the elm leaf beetle is closing in on two additional generations per year (see Fig. 4).

Predictions based on the CGC M3.1 resulted in the smallest increases about 75% of the time, whereas predictions based on the CSIRO Mk3.5 resulted in the largest increases about 75% of the time although,
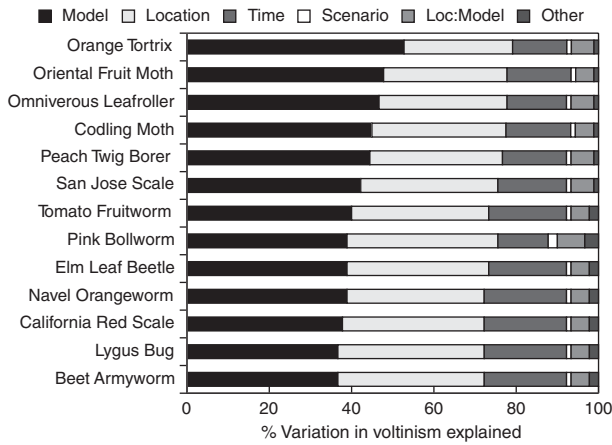
Fig. 3 The relative magnitude of various sources of uncertainty in the predicted voltinism of 13 economically important agricultural pests of California. Each bar represents the total variance in results for a specific pest, partitioned into variance explained by model, location, time, scenario, location model interaction and other, where other represents all remaining interactions.

clearly, the pattern was not universal. It would be difficult to intuit these results from an examination of Fig. 2, which shows how mean values can sometimes be misleading.

The predictions derived from the projected baseline temperature data differed considerably from those derived from historical temperature data (Fig. 5). For northern California, predictions based on historical data were higher than for all three climate models,

although particularly so for the GFDL CM2.1 model. For southern California, predictions were again higher when based on historical data than for the GFDL CM2.1 model, but were lower for the CSIRO Mk3.5 model. Predictions for the CGC M3.1 model in the southern location were the most similar between historical and projected temperature data, with only minor discrepancies. We present these differences for information only. While it would be possible to apply a 'correction' to the baseline results, to minimize this difference, we feel such an approach is ill-advised. The important comparison in this work is the difference between the predictions that result from using the baseline and future climate projections (e.g. Fig. 4). Baseline projections are generated using the same GCMs as the future projections, and therefore, any uncertainty due to differences between model projections and actual climate are not confounded with the assessment of climatic change *per se* (as they are for example in Luedeling *et al.*, 2011). While applying a 'correction' to the baseline is mechanically possible, that same correction should not be applied to the future predictions, as there is no reason to believe that the bias between model projections and future climate will be of the same size or direction as the differences between the baseline and the historical climate. As this is the case, there is nothing to be gained by 'correcting' the bias in the baseline results. It is sufficient to simply note these differences for additional perspective in considering the implications of predicted results.
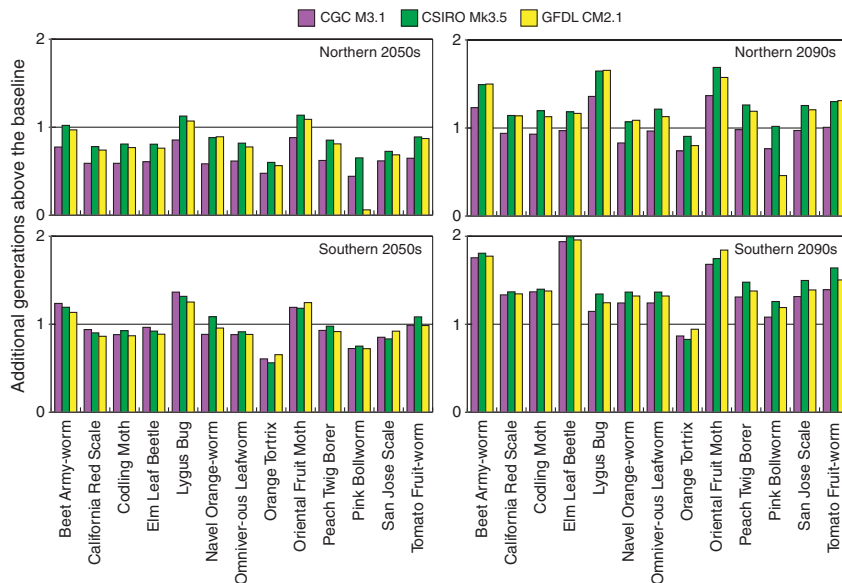

Fig. 4 This figure depicts the predicted increase in the number of generations, calculated as the predicted number of generations in the future minus the number of generations predicted under the baseline condition for the northern and southern locations.
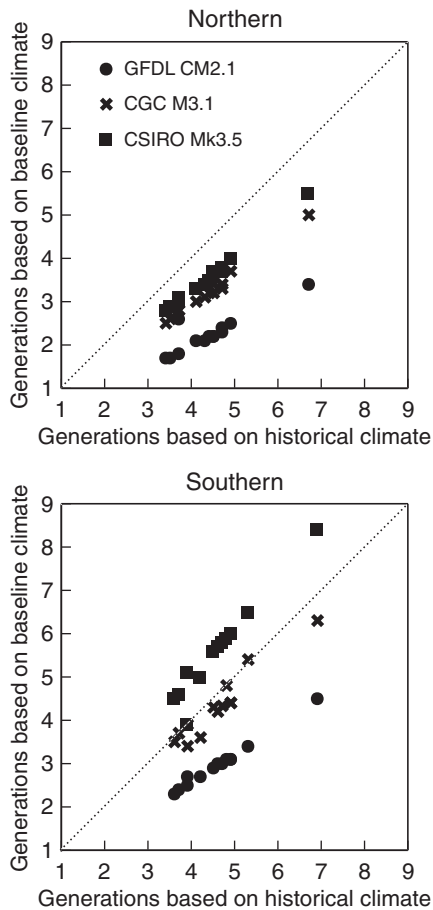
Fig. 5 Comparison of predictions based on historical climate data to those based on the baseline time period for each climate model. GCM-based climate projections for the baseline period uniformly underestimate voltinism for the northern location and perform differently for the southern location.

Discussion

Conclusions about California pests

Luedeling *et al.* (2011) recently conducted an assessment of four California pest species, including two considered in our work, using similar degree-day models. There are a number of significant differences between Luedeling *et al.*'s work and ours. Luedeling *et al.* consider predictions for the whole of California, although the focus is on the Central Valley area. A notable difference is that although Luedeling *et al.* used projections from three GCMs (CSIROMK3.0, HadCM3 and MIROC3.2), they averaged over the results from each GCM before analysing them, thus avoiding an analysis of the impact of climate model choice (but see their Fig. 3). Rather than use the baseline output for each climate model as the 'control condition',

Luedeling *et al.* used a specially generated comparison dataset based on historical climate data. Despite these differences, Luedeling *et al.*'s qualitative conclusions for the four species they considered are similar to the 13 we consider in the present work. They predicted increased generations, but because of the differences in approaches to baseline conditions and Luedeling *et al.*'s use of downscaling and averaging of GCM-specific results, plus the differences in GCM choice, we are not able to make more quantitative comparisons between the two studies.

In this study, the number of degree-days per year is predicted to increase over the next century for all 13 pest species investigated, regardless of the climate projection utilized to generate the predictions. As we pointed out earlier, whether the increased accumulation of degree-days results in an additional generation is less clear. The occurrence of additional complete generations is only a robust conclusion for the southern location at the end of the century. Much will probably depend on how agricultural practices change in response to the changing climate.

Model choice explained between 37% and 54% of the variance in predictions of voltinism across the 13 pest species. This is greater than the variance explained by choice of location or time period, and substantially greater than scenario, which explained on average a mere 1% of the variance in results. The discrepancy between the variance explained by GCM choice and by emissions scenario choice is particularly surprising, as different scenarios are expected to yield different predictions of biological impacts by virtue of their nature (Table 2).

Climate scenarios are not predictions or forecasts; rather, they are plausible ideas of what the future might look like. The four families of climate scenarios are based on plausible changes in demography, socio-economic development and technological development; changes that are poorly understood and very difficult to predict (Nakicenovic *et al.*, 2000). Due to this considerable uncertainty surrounding future greenhouse gas emissions, the inclusion of multiple scenarios is often prioritized over the inclusion of multiple models in impact studies. This study shows that, at least in certain systems, the inclusion of multiple models can be more important than the inclusion of multiple scenarios in terms of gaining a more complete understanding of the possible impacts of climatic change. We certainly would not suggest an abandonment of the multiple scenario approach; the logic behind the inclusion of multiple scenarios is well supported (Nakicenovic *et al.*, 2000). What we would advocate, based on these results, is to always include multiple GCM-scenario combinations (see e.g. Kriticos *et al.*, 2009; Mika & Newman, 2010; Mika *et al.*, 2008; Newman, 2006; Thuiller, 2004)

to ensure that both sources of uncertainty – model and scenario – are accounted for.

Although addressed less often than scenario uncertainty, there is also uncertainty associated with GCMs. As previously mentioned, there are currently 23 GCMs used by the IPCC (Randall *et al.*, 2007). These models vary in the number and type of processes and feedback mechanisms that are incorporated, whether processes are represented mechanistically or phenomenologically, in their spatial and temporal resolution, *etcetera* (Randall *et al.*, 2007). Thus, each model represents a different abstraction of the climate system. Although certain models perform better for specific measures of fit, no single model consistently performs at the top; none of these models are considered to be any "better" than any other (Bader *et al.*, 2008). Accordingly, researchers engaging in biological impact studies are encouraged to use several models (Mika *et al.*, 2008; Nakicenovic *et al.*, 2000; Newman, 2006), a recommendation that is again supported by the results of this study.

Location also had a substantial effect on the impact of climatic change on the pest species, explaining 33% of the variation in the response. A location effect in and of itself is not surprising; warmer temperatures in the south would be expected to contribute to a higher number of generations per year. Indeed, the further apart (along the latitudinal gradient) the two locations are located, the more variation we would expect 'location' to account for. More interesting, however, was the presence of a substantial location by model interaction, suggesting that the influence of model choice on pest response may be at least partially location specific. Referring back to the projected minimum temperatures (Fig. 2), there is a greater discrepancy between the northern and southern temperatures for the CSIRO Mk3.5 model than for either of the GFDL CM2.1 or CGC M3.1 models. This inconsistency likely accounts for the substantial interaction between location and model.

It would be premature to make a sweeping conclusion declaring model choice to be the primary factor in determining the impacts of climatic change on agricultural pests in California, as we have only investigated three of 23 possible GCMs here. Indeed, it is possible that one, or even two, of the models used here are anomalies, and that the remaining 20 GCMs would yield similar predictions of voltinism, although we doubt that this is the case. What these results do emphasize is that when studies use only a single GCM, their conclusions should be interpreted with caution, as they may be heavily 'model dependent'. Decisions formed on the basis of predictions made by impact studies – in the form of policies, mitigation strategies,

etc. – may play a significant role in shaping the future. Thus, overconfident predictions of the impact of climatic change have the potential to be "expensive failures" (Knutti, 2010). If biologists are to wisely inform policy makers regarding the impacts of climatic change, it is imperative that uncertainty in model projections be quantified and reported in biological impact studies.

Model criticism

It could be argued that this modelling approach overly simplifies the problem of predicting the response of agronomic pest species to climatic change. The point of a model is not to reproduce nature in mathematics, the point is to simplify nature, to abstract it to capture a few essential features. The justification for this abstraction lies in the incomprehensible complexity of even these reasonably simple agricultural systems (compared with more natural and extensive ecosystems). Note that this is equally true of reductionist experimental approaches, and so it is not limited to models *per se*. "The fact that a model does not and cannot consider every detail of the system it represents is irrelevant, what matters is whether this vast simplification contains the essential mechanisms that are known or thought to drive the system dynamics. We cannot always know, *a priori*, whether this is the best simplification, just as we cannot know whether we have included all possible interactions in an experiment." (Hoover & Newman, 2004). Degree-day models have a long history and a proven track record in pest management, which we feel is sufficient evidence that they capture some important aspects of the biology of insect pests, and are therefore a useful abstraction. Nevertheless, it is worth reminding ourselves of what the models cannot do. In this section, we briefly consider the limitations of this and other modelling approaches to provide some perspective on our results, and to see how this approach compares to others we could have used.

In our view, the most significant limitations of this approach for studying herbivorous arthropods are (1) dependence solely on temperature means that the models are not well suited for considering interactions between changing temperature, precipitation and rising CO_2 concentrations (Robinson *et al.*, 2012); (2) these models cannot capture the feedback from the changing host-plant quality that will certainly occur under these conditions (Robinson *et al.*, 2012); and (3) they assume that the current upper and lower developmental thresholds for each species will remain constant through time (i.e. that there will be no local adaptation to the changing climate; see Newman *et al.*, 2011 for further discussion). These problems are not entirely

unique to degree-day models; bioclimatic envelope models and ecological niche models both suffer from problems (2) and (3), and although they are capable of incorporating aspects of climate beyond daily minimum and maximum temperatures, they are still ill-suited to dealing with interacting effects, particularly under changing climatic conditions. Physiologically based mechanistic models suffer from (3) but are largely able to overcome problems (1) and (2) and should be the preferred approach except that they are vastly more difficult to develop and implement, and while they may be more useful for investigating interactions and feedback mechanisms, they are not necessarily better at forecasting insect population dynamics (Newman, 2004, 2005, 2006, Newman *et al.*, 2003). The simplicity of degree-day, bioclimatic envelope and ecological niche models gives them a certain heuristic value, allowing us to focus on a single problem at a time (Mika & Newman, 2010; Mika *et al.*, 2008). Despite the drawbacks inherent in such extreme reductionist approaches, there is still a role for such models in our overall approach to predicting the biological impacts of climatic change.

Acknowledgements

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Appendix S1. Growing Season Length (Ziter *et al.* 2012, *Global Change Biology*).

Table S1. Growing Season Length in the Northern and Southern Locations, for the A1B scenario. Note that some of the model outputs for this variable, for the southern location, were not available on the Canadian Climate Change Scenarios Network website.

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