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REVIEW

Complexity in climate-change impacts: an analytical framework for effects mediated by plant disease

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The impacts of climate change on ecosystem services are complex in the sense that effective prediction requires consideration of a wide range of factors. Useful analysis of climate-change impacts on crops and native plant systems will often require consideration of the wide array of other biota that interact with plants, including plant diseases, animal herbivores, and weeds. We present a framework for analysis of complexity in climate-change effects mediated by plant disease. This framework can support evaluation of the level of model complexity likely to be required for analysing climate-change impacts mediated by disease. Our analysis incorporates consideration of the following set of questions for a particular host, pathogen, host–pathogen combination, or geographic region. 1. Are multiple biological interactions important? 2. Are there environmental thresholds for population responses? 3. Are there indirect effects of global change factors on disease development? 4. Are spatial components of epidemic processes affected by climate? 5. Are there feedback loops for management? 6. Are networks for intervention technologies slower than epidemic networks? 7. Are there effects of plant disease on multiple ecosystem services? 8. Are there feedback loops from plant disease to climate change? Evaluation of these questions will help in gauging system complexity, as illustrated for fusarium head blight and potato late blight. In practice, it may be necessary to expand models to include more components, identify those components that are the most important, and synthesize such models to include the optimal level of complexity for planning and research prioritization.

Keywords: cereal head blight, disease risk, ecosystem services, *fusarium graminearum*, potato late blight, *phytophthora infestans*

Introduction

Anticipating and responding to the effects of climate change presents many challenges, including the fundamental one of understanding how climate change will influence crops, other plants, and the ecosystem services (MEA, 2005) they provide. Reductionist approaches to biology are unlikely to be adequate for fully understanding climate-change effects. Some important components of plant systems may be simple enough for reductionist approaches to provide at least a 'first-order approximation'. However, many components are likely to be far too complex for simple models to provide suitable approximations. The recent economic downturn exemplifies the potentially disastrous results from incomplete understanding of systems. Economic models have often included the assumption that there will be counterbalancing forces to maintain desirable equilibria (Rosser, 1999), and that past regulating mechanisms will continue to operate into the future. The near-global economic recession since 2008 illustrates how inability to effectively predict and manage system complexity can yield catastrophic results (May *et al.*, 2008).

System complexity has many definitions, beyond a system being 'complicated'. Mitchell (2009) gives a lively

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overview of definitions of complexity, including features potentially associated with higher complexity, such as larger genomes, higher entropy, higher algorithmic information content, greater logical depth, greater thermodynamic depth, higher fractal dimension and higher degree of hierarchy (Allen & Starr, 1982). Here we discuss complexity in terms of the amount of information required to predict outcomes, an approach related to the concept of statistical complexity. One measure of the current level of scientific understanding of a system is our ability to predict future outcomes in the system (Jeger, 2008). An example of a 'low-complexity' system would be one that is suitably described by a model such as the following. 'If temperature increases by 2°C on average, maize will photosynthesize *X*% more efficiently in a given country, and thus maize productivity will increase by *Y*%.' It will be important to determine how well such simple models describe systems, in terms of criteria such as the percentage of variation they explain, and their accuracy and precision.

Conversely, some system components may not be needed to model long-term effects. A common problem in scaling up the results of short-term empirical studies is the erroneous assumption that certain individual components of a system are equally important across all levels of integration (Rabbinge, 1989). In practice, the overall response of a system to variation in one of its components may average out over scenarios. As a result, a suitable approximation of effects can be obtained without explicitly including that component. Sensitivity analyses may reveal which model components have important impacts on outcomes. For example, it may sometime be useful to partition host-plant resistance to pathogens and the stages of infection into a number of subcomponents (Kranz, 1990). When evaluating the effects of climate change, for some pathosystems all these components may be affected similarly, in which case it would be appropriate to use a single parameter to represent the effect of resistance and how the effect of resistance changes with climate. However, in other pathosystems particular resistance components may need separate treatment for adequate prediction.

System components such as plant pathogens and plant herbivores have the potential to sharply reduce the percentage variance explained by simple models of the effects of climate change on plant productivity. Yet the effects of climate change on plant systems are often evaluated without due consideration of plant diseases and herbivores (Gregory *et al.*, 2009). Plant diseases and animal pests have important impacts on agricultural systems; for example, chronic yield losses to plant diseases (i.e. yield loss not attributable to acute or emerging disease problems) are estimated at over 10% of rice yield in tropical Asia (Savary *et al.*, 2006). The average global yield loss to disease is estimated at 16% (Oerke, 2006). In multispecies systems such as plant disease, climate can affect each species individually, as well as influencing the interactions between species (e.g. Legrève & Duveiller, 2010). Rapid reproduction in plant pathogens and herbivores can amplify the effects of weather change and variability. Climate-change-driven shifts in agricultural patterns and practices add another layer of complexity (Savary *et al.*, 2005; Valdivia *et al.*, 2010). Here we focus on plant disease, but similar forms of complexity will hold for insect herbivores and weeds, as well.

Our objective in this paper is to develop a framework for evaluation of complexity in the effects of climate change mediated by plant diseases. Climate-change effects on plant disease are interesting in their own right, as are the effects on all biological communities, but plant disease merits particular attention because of its important impacts on ecosystem services such as food production. Thus, we address both climate-change impacts on plant disease and the broader resulting impacts on ecosystem services. This instrument can be used to evaluate complexity in the context of a geographic area, a production system, a particular crop species, or a particular pathogen species. It is intended as a tool for identifying system components that may require particular attention for effective evaluation of climate-change impacts.

'Simpler' models of disease risk

The impact of climate on plant disease through weather patterns has been studied in detail for several important plant diseases, particularly at smaller scales (Coakley *et al.*, 1999; Garrett *et al.*, 2006), and also at larger scales in some cases (e.g. Luo *et al.*, 1998). In some cases it is possible to predict with reasonable confidence whether a given disease will become more or less important at a given location (typically, a field) as a function of weather variables. Climate change will clearly have direct effects on plant disease epidemics. Effects of variation in temperature on life cycles (Scherm & van Bruggen, 1994) are well established. Quantifying them, however, requires additional careful, disease-by-disease experimentation and analysis, because of differing nonlinear relationships between temperature and the rate of disease development among pathosystems.

Another example of direct effects is the effect of water supply and drought stress, which is becoming better documented in, for example, rice (Savary *et al.*, 2005). Water stress and heat stress in plants are predicted to increase in many regions, and this is likely to influence plant disease epidemics. An important component of the climate-disease interaction is mesoclimate and plant-growth effects on canopy microclimate (Monteith, 1972; Huber & Gillespie, 1992). Further, physiologically stressed plants often may be more susceptible to some diseases. Stressed plants may often be exposed to higher attack rates, either as a result of physical damage allowing access to pests, or as a result of physiological diversion of resources from defence to maintenance. In other cases, however, drought stress may induce resistance reactions. The complexity of this interaction will be an important component for consideration in predictive models, as well.

For example, dry root rot of chickpea (caused by *Rhizoctonia bataticola*) is emerging as a potential threat

to chickpea cultivation in rainfed environments, because the host plant is predisposed to infection by moisture stress and higher temperatures during the flowering to pod filling stage (Pande *et al.*, 2010). Diseases of rainfed crops, such as phytophthora blight (PB, caused by *Phytophthora drechsleri* f.sp. *cajani*) in pigeon pea and dry root rot in chickpea, can cause almost 100% crop loss as a result of weather extremes associated with climate change (Pande *et al.*, 2010). In the Deccan Plateau of India, the frequent resurgence of PB corresponds with changing rainfall patterns in the last decade (Sharma *et al.*, 2006; Pande & Sharma, 2009). When temperatures are between 24 and 28°C and rainfall >300 mm within a week during the crop season, PB can completely destroy the pigeon pea crop regardless of crop cultivar. Spot blotch of wheat, caused by *Cochliobolus sativus*, is also affected by stress factors, and disease incidence and severity are likely to increase in the eastern plain zones of South Asia (Sharma *et al.*, 2007).

Typical disease forecasting models based on weather do not incorporate larger-scale processes or complexities that may lead to higher or lower levels of inoculum availability and pathogen dispersal (Seem, 2004). Nor do they incorporate the large effects of increased scarcity of water, labour, energy and other natural resources on cropping practices and systems (Savary *et al.*, 2005). Most forecasting tools are meant for tactical decisions within a season (e.g. Butt & Jeger, 1985; Rossing, 1993), or at best for strategic short-term decisions (Esker *et al.*, 2006); a priority now is to develop methodologies for strategic long-term decisions (e.g. Teng & Savary, 1992) that are congruent with the unfolding consequences of climate change and other global change factors.

To enhance analyses of the effects of climate change, we evaluate scenarios that involve thresholds, interactions and feedback loops (Garrett, 2008). Discontinuities and thresholds (Garrett & Bowden, 2002; Gilligan & van den Bosch, 2008) can occur, such that disease is constrained for some ranges of weather variables and then quickly released from constraint when weather variables shift by a relatively small amount.

The translation of disease intensity into qualitative or quantitative crop losses is nonlinear and depends on a damage function (Zadoks, 1985). Addressing the consequences of epidemics on crop losses inevitably entails addressing injury mechanisms (Willocquet *et al.*, 2004) and thus, also, host physiology (Ayres, 1981). This represents another layer of complexity. One approach to predicting diseased-related crop losses resulting from climate change is to use dynamic simulation models of disease development and subsequent crop loss with climate change as a driver.

Uses of plant disease models in climate-change scenario analysis

Analysis of plant disease in climate-change scenarios may have several uses. For groups with responsibilities for long-term planning in agriculture, such as national agricultural departments and the Consultative Group on International Agricultural Research (CGIAR), the need to prioritize research and extension activities to address future needs is acute. In general it may take at least 10 years to develop an annual crop variety resistant to any given disease, and much longer for perennial crops such as banana and fruit trees. The time required for an improved variety to be widely adopted in the developing world may be much longer, depending on the cropping system. Research in the CGIAR system has strongly benefited agriculture in the developing world, but with an estimated time-lag of about 40 years (Pardey *et al.*, 2006). Scenario analysis to address the need for advance planning will tend to focus on which diseases will become more important where, what types of impacts different management strategies may have, and what institutions will be needed to support these strategies.

A second use may be to document quantitatively the importance of climate-change mitigation. If analyses show that a disease or set of diseases will become more or less important under climate change, this may be used as part of a general argument in debates about how heavily policy should prioritize climate-change mitigation and adaptation. It may also be of interest to evaluate evidence for already existing effects of climate change on plant disease epidemics, but the many interacting factors that result in plant disease make clear evidence for such effects challenging to obtain (Garrett *et al.*, 2009a). A related application is the assessment of how climate-change mitigation may benefit from plant disease management (Mahmuti *et al.*, 2009).

An evaluation of the complexity of systems' responses to climate change can also be used for research prioritization and evaluations of the confidence in future scenario analyses. Research prioritization may address both problem solving and problem identification. Priorities for problem solving in the short run may focus on systems where simple models suggest large effects of climate change. For example, where a disease is known to be much more problematic at higher temperatures, and temperature is predicted to increase, management for this disease may be a logical priority for research to improve management techniques. On the other hand, research for problem identification may logically focus on evaluation of systems where complexity makes it relatively more difficult to assess future scenarios. These systems might be particular diseases, hosts or environments. Evaluating absolute levels of complexity is a great challenge, but may be necessary for developing estimates of confidence associated with analyses of climate-change effects. The greater the inherent system complexity, the lower the confidence in analyses based on simple models. Even when more complex models are used, confidence in predictors will still tend to be lower for complex systems than for truly simple systems because of the propagation of error associated with each model component.

Levins (1966) presented a well-known review of the potential goals for models – generality, realism and precision – and the idea that attaining all of them

simultaneously is generally not possible. The need to consider models as research tools in successive phases (Penning de Vries, 1982) derives from this conflict of objectives. In plant disease epidemiology, accuracy and precision have been common goals for short-term tactical modelling applications. For example, accuracy and precision are necessary for a model to be useful in providing recommendations for pesticide applications in a particular field. In the context of long-term strategies, that deal broadly with agriculture and other ecosystems, generality may be a more important modelling goal, so that models can be applied across a range of scenarios being considered. Generality is also needed when evaluating scenarios for pathogens that have received little research attention, but which are related taxonomically and perhaps functionally to other more-studied pathogens. Realism is often desirable, but the inclusion of increasing numbers of parameters also increases the propagation of errors associated with each parameter estimate (Nagy *et al.*, 2007).

Climate data as input for plant disease models

The relevant level of complexity in the climate scenarios used in modelling is also an important issue (Shackley *et al.*, 1998). The utility of climate-change scenarios may be low when based on general circulation models (GCMs) with low spatial resolution [for example, 2·5° latitude (250 km) and 3.75° longitude (350 km)]. Climate-change predictions are generally for increases in the mean global temperature, as well as changed variability, leading to changes in crop production. Precipitation patterns are commonly expected to exhibit increases in the differences between dry and rainy environments, with more frequent extremes. Changes in the features of rainy seasons may include onset, intensity and soil moisture, as demonstrated in the Andes (Seth *et al.*, 2010; Thibeault *et al.*, 2010). Agricultural systems are highly responsive to such climatic changes: farming systems and cropping practices are adapting to new conditions, and as new crops are grown in a given region there may be less knowledge and experience with their cultivation, with important consequences for plant disease epidemics (Savary *et al.*, 2005; Valdivia *et al.*, 2010). A key challenge is to disentangle the direct contribution of climate change *per se* and its indirect effect through agricultural adaptation (Coakley *et al.*, 1999). There are two dominant trends in adaptation: many farmers seek to reduce agricultural risks by enlarging the scale of operations and intensifying production systems, whilst in alternative agricultural systems adaptation may be through the use of ecological buffering systems, including improved soil organic matter and water-holding capacity, minimizing potential drought effects (Lotter *et al.*, 2003; Teasdale *et al.*, 2007). In developing-country agriculture, infrastructural limitations (roads, educational systems, communication networks) and policy shifts lead to imperfect market signals, which must also be taken into account. Climate change may increase the possibilities for new crops, but also increase the fear and lack of control in dealing with plant and animal diseases, as a result of lack of access to knowledge and limited ability to access and/or purchase inputs in a timely matter (Valdivia *et al.*, 2010). Complete evaluation of these important factors represents a very large, multidisciplinary endeavour.

Assessments of climate and weather influence on crop diseases depend on time and spatial scales. Weather variation during hours or days can be critical for assessing the weather impact on some diseases, whereas in some cases the average climate over weeks and months can be the main determinants. The response of a pathogen or insect pest to average environmental variables such as weekly or monthly temperatures can be strongly affected by the amplitudes of daily oscillations in those variables (Scherm & van Bruggen, 1994). In many countries, daily records for temperature, humidity and precipitation, etc., are available at the local scale, and there are established methodologies available for estimating hourly values from daily values [cf. Parton & Logan (1981) for temperature, and Eckersten (1986) for humidity] to provide crop disease models with input. For assessments on the regional scale there are methodologies available for interpolation between locations, regularly used by weather services, for example to replace missing data. Also, satellite images provide valuable information for regional assessments of the climate and weather impact on crop diseases. The existence of corresponding information about disease is often a limiting factor, with some exceptions. Long-term trials such as Broadbalk at Rothamsted Research, Harpenden, UK have shown that air quality and human activity were associated with a shift in prevalence of wheat diseases caused by *Mycosphaerella graminicola* (*Septoria tritici*) over *Phaeosphaeria nodorum* (*Stagonospora nodorum*) over the course of decades (Bearchell *et al.*, 2005).

To assess the effects of climate-change scenarios (cf. SOU, 2007), crop disease models need climate inputs of the same high temporal and spatial resolution used for their calibration and parameterization, usually weather records at a daily or hourly temporal resolution and plot- or field-level spatial resolution. However, climate-change assessments are made for large temporal and spatial units, and their reliability decreases in the context of high resolution analyses. There are three main approaches to attack this problem. Climate inputs may be downscaled to finer resolution (cf. weather generators; Semenov & Stratonovitch, 2010) and used as input for the crop disease models. Estimates of disease risk may be interpolated for areas between locations with data. Or, crop disease models may be calibrated for coarser resolution input weather data (AH Sparks, GA Forbes, RJ Hijmans, KA Garrett, unpublished data). All methods introduce uncertainties to the assessments. The increased uncertainty of climate-change scenarios at finer resolution may make it

more meaningful to assess average future climate-change impacts over long periods, such as 30 years, rather than making transient assessments.

An assessment framework

The proposed framework for assessing potential effects of climate change on plant disease includes a rubric for exploring predictors that may be important model components depending on the complexity of the system (Table 1). The first three questions in the rubric address system characteristics that will influence plant disease, whilst the others address characteristics that will influence the impact of plant disease on other diseases, crop yield or the environment. The traits that these questions address are not independent, so a single pathosystem trait may lead to positive responses in more than one category.

1. Are multiple interactions important?

For plant disease, a 'null hypothesis' based on the absence of multiple interactions could almost always be rejected. But there are degrees of complexity in the number and types of interactions. Microbial communities may interact to produce disease-suppressive soils, or other forms of biological control. Range shifts resulting from climate change may produce new combinations of pathogen and vector species, and the potential for new hybrid pathogens (Brasier, 2000). Gilman *et al.* (2010) give examples of how climate shifts may affect different types of community interactions as environments move outside the ancestral conditions of the different species. Generalized relationships such as specialist enemy and victim pairs, mutualisms, exploitative competition, food chains, apparent competition and keystone predation may all change as one species may adapt more readily to the new climatic conditions than another.

There may be interactions among agricultural systems and between agricultural and natural systems, such as sharing of pathogens among systems. For example, the generalist fungal pathogen *Macrophomina phaseolina* (which has a greater detrimental effect under drought stress) has closely related populations associated with hosts in tallgrass prairie, maize, sorghum and soybean (Saleh *et al.*, 2010), indicating the potential connectivity of these systems, where epidemics in one system may affect epidemics in others. This pathogen's effects are exacerbated by drought stress and rotations of cowpea and millet in the Sahel region, but can be reduced when fonio (*Digitaria exilis*) is included in the rotation (Ndiaye *et al.*, 2008). Another example of a potential increase in disease as a result of interactions of farming systems and climate change is the risk of wheat and barley fusarium head blight (FHB) as a consequence of the expansion of maize production (as may result from longer growing seasons), in particular when maize is grown in no-till systems in

Table 1 A framework for evaluating complexity in climate-change effects mediated by plant disease, indicating scenarios where system complexity is potentially lower or higher

	Lower complexity	Higher complexity
1. Are multiple biological interactions important?	A single pathogen species 'acting alone' causes disease in a single plant species	Microbial communities, vector communities, and/or complex landscapes influence disease outcomes
2. Are there environmental hresholds for population responses?	Pathogen population responses to climate variables are constant throughout the relevant range	Pathogen population responses change suddenly at particular thresholds
3. Are there indirect effects of global change factors on disease development?	The relationship between climate variables and disease risk is unrelated to other factors	Global change factors, such as changes in land use, water, transportation and/or markets, influence the relationship
4. Are spatial components of epidemic processes affected by climate?	Disease risk at a given location is not influenced by disease risk at other locations	Climate may influence the likelihood of disease spreading among locations
5. Are there feedback loops for management?	Management tools have the same level of efficacy despite changes in other system components	Management efficacy changes greatly with changes in the system
6. Are networks for intervention technologies slower than epidemic networks?	Disease is already present in relevant areas, or is very well understood and readily managed by farmers	Disease moves to new areas where farmers do not have tools and knowledge for management; there are no knowledge networks that correspond to the epidemic networks
7. Are there effects of plant disease on multiple ecosystem services?	Disease has impacts only on yield of a single host plant species	Disease may impact other plant species and/or health of humans, other animals, and soils
8. Are there feedback loops from plant disease to climate change?	Disease is affected by climate change, but has no impact on climate change	Severe epidemics as a result of climate-change affect climate-change factors such as soil water holding capacity, erosion, and/or photosynthetic capacity

short rotation with wheat (Zadoks & Schein, 1979; Dill-Macky & Jones, 2000). Models of climate impacts on individual plant species may need to be linked to give useful predictions.

2. Are there environmental thresholds for population responses?

The complexity of climate-change effects on plant disease results in part from multiple potential effects climate has on the development of plant diseases. Different stages in the development of an airborne pathogen can be affected differentially by temperature, light intensity, relative humidity, free moisture, etc. Different stages of soilborne pathogens are affected by short-term changes in soil moisture and (less so) in temperature. Although climate change is often expressed in terms of average annual, monthly or weekly temperature or rainfall, plant pathogenic organisms and their vectors respond instantaneously to environmental conditions, and have short generation times, so mean values of environmental variables may have reduced predictive power for their growth or development (Scherm & van Bruggen, 1994; Wu *et al.*, 2002). As the relationship between pathogen dynamics and temperature, for example, is generally nonlinear, the response to temperature fluctuations can be very different from the response to constant temperatures with the same mean (Scherm & van Bruggen, 1994; Semenov *et al.*, 2007). Thus, the dynamics of disease progress can be understood better when we consider the response time for the different developmental stages of the pathogen in relation to the dynamics of environmental conditions rather than average conditions. Techniques for evaluating signs that a system may be approaching a critical threshold may find application in this context (Scheffer *et al.*, 2009).

Population thresholds may produce larger impacts from climate shifts than would otherwise be anticipated. For example, the Karnal bunt pathogen experiences an Allee effect, or reduced per capita reproduction at lower population sizes (Garrett & Bowden, 2002). In this case, the reduced per capita success at low population levels is caused by the necessity of different mating types encountering each other for reproductive success. If climatic conditions change such that weather variables are shifted to support populations above an Allee or comparable threshold, the problems caused by the pathogens or insect pests may increase by an amount greater than would have been predicted in a model ignoring this type of complexity. Conversely, if weather variables are shifted to support only lower populations, the decline in the problem may be greater than anticipated. Other examples would include Allee effects in arthropod pests and vectors of plant pathogens when these vectors must find mates or when they benefit from changes to the microenvironment produced by larger population sizes. For example, wheat curl mites, the vector of *Wheat streak mosaic virus* and other plant pathogenic viruses, when present in sufficient numbers, induce curling in wheat leaves, and thus a sheltered environment for the mites.

3. Are there indirect effects of global change factors on disease development?

A number of global change factors may influence the relationship between climate and disease. Increased transportation flows have important effects on the dissemination of pathogens to new areas. Changes in human population densities, and resulting impacts on availability of labour and water, may strongly influence disease impacts (Savary *et al.*, 2005). Patterns of investment in agricultural research may leave 'orphan crops' such as quinoa and cowpea with less support, despite the crop species being particularly important in some regions (Nelson *et al.*, 2004). Conversion to reduced tillage systems as part of conservation agriculture programmes (Hobbs *et al.*, 2008; Giller *et al.*, 2009) may increase disease risk (Bockus & Shroyer, 1998). For example, in wheat-based systems (providing the food base of nearly a billion people in South Asia), the expansion of conservation agriculture is expected to increase the incidence and severity of stubble-borne diseases such as tan spot and septoria leaf blotches (Savary *et al.*, 1997; Duveiller *et al.*, 2007).

Changes in policy may also influence the relationship between climate and disease. For example, Sweden and other European countries have previously implemented policies to reduce overproduction of wheat, such that a percentage of acreage should be under fallow not to be broken before 1 July. Fallow fields with volunteer wheat provided habitat for the leaf hopper *Psammotettix alienus,* which is a vector for *Wheat dwarf virus* (WDV) (Lindblad & Waern, 2002). Increasing autumn and winter temperatures would favour the survival of the vector and such policies would then contribute more to WDV infections. In risk areas, tillage is still desired to avoid WDV in remaining plant cover in all crop rotations, but especially in rotations where wheat follows wheat. Another example of policy impacts is removal of barberry to reduce stem rust risks. Since the late 1990s an increase in the occurrence of oat stem rust *Puccinia graminis* f.sp. *avenae* has been observed in eastern central Sweden. This is believed to have connections with the barberry eradication law which was repealed in 1994. With increasing temperature, stem rust epidemics could develop faster and provide higher levels of initial inoculum produced locally. If long-distance dispersal is not required to initiate epidemics, stem rust epidemic could become more severe, depending on the conduciveness of the environment for disease development during the cropping season. A similar effect may be observed for wheat stripe rust *P. striiformis*, because it was recently discovered that this rust species also has its perfect stage on barberry (Jin *et al.*, 2010).

Whilst the effects of climate change on weather will influence plant disease, these changes in weather are and will continue to cause shifts in cropping seasons and areas as well (e.g. Valdivia *et al.*, 2010). It is challenging to pre-

dict these shifts in crop growing areas or seasons as a result of complex social, economic and agricultural interactions. Crop growth models can be used to project growing seasons and areas using model inputs such as total solar radiation, minimum and maximum temperature, rainfall and irrigation; or projected data based on climate-change models (Tubiello *et al.*, 2002). However, because farmers may plant crops in areas or time periods so as to avoid disease (Thurston, 1990), crop growth models may misrepresent future growing seasons or areas because normally they model the optimal conditions for the crop and do not make allowances for disease or other pests. This asynchrony can lead to model outputs for disease risk that are out of sync with the time when crops are in the field and will be experiencing disease risk. Care must be taken when projecting the effects of climate change on plant disease to ensure that the temporal parameters for both the pathogen and the crop are congruent for more accurate results. Using the FAO ECOCROP I database (FAO, 2004), potato can potentially be grown over most of the global surface using irrigation. However, work by Hijmans (2001) shows that the area of potato production is more limited. These are issues that make an interdisciplinary approach necessary.

4. Are spatial components of epidemic processes affected by climate?

Invasive pathogens may have radical effects on natural or agricultural ecosystems; global change through invasions interacts with climate change in particularly important ways for plant pathogens. Pathogen invasions are likely to be facilitated by a number of factors, including availability of pathogen propagules, the adaptability of pathogens, and the availability of open niches (McRoberts *et al.*, 2003) and disturbance, all of which are likely to be influenced by climate change. Invasion of an ecosystem by a pathogen is also partially dependent on the health status of the system, as indicated by a dynamically balanced and diverse community of organisms, stability and resilience after disturbances, minimal losses of nutrients and energy, and sporadic outbreaks of pests and diseases (van Bruggen & Semenov, 2000). The extent of oligotrophy, in terms of easily available carbon sources and mineral nutrients, largely determines the health status of an ecosystem. This holds not only for aquatic ecosystems, but also for terrestrial and soil ecosystems. Eutrophication of ecosystems is widespread, but the consequences, such as a drastic reduction in biodiversity and increased instability, are better understood for aquatic than for terrestrial ecosystems (Scheffer & Jeppesen, 2007). Eutrophication is often not considered a part of global climate change as such, but it also originates from excessive use of natural resources and disposal of waste products. The interrelations and feedback mechanisms between climate change and eutrophication deserve more research, especially with respect to invasion by existing and emerging pathogens. For example, the decline of a pathogen population in soil was more irregular in eutrophied compared to more oligotrophic soils (Semenov *et al.*, 2008).

Long-distance dispersal of pathogens occurs naturally on global and continental scales (e.g. Stackman & Harrar, 1957; Van der Plank, 1967; Brown & Hovmøller, 2002), and via movement by people or in plant material (Anderson *et al.*, 2004). Dispersal of pathogen inoculum is crucial to the development of many plant disease epidemics, such as soybean and wheat rust fungi that overwinter in regions with milder climates and annually re-invade cooler regions (e.g. Li *et al.*, 2010). Nonetheless, research into the potential effects of climate change on plant disease has often focused on development of disease *in planta*. This is in part because of the physical and biological complexity of inoculum dispersal processes (e.g. Aylor *et al.*, 2001), the difficulty of collecting empirical dispersal data at relevant spatial scales, and the mathematical complexity of atmospheric dispersion models. Consequently, there is a lack of information in the literature concerning the potential impact of climatic variation on the aerobiology of plant diseases. Potato late blight (caused by *Phytophthora infestans*) is an example of a pathosystem where aerobiological models have been constructed and validated (Skelsey *et al.*, 2008, 2009a,b,c, 2010). In this model, dispersing sporangia encounter different wind and turbulence conditions, depending on the time of day of release. Once released, these spores must escape up through the canopy to become available for long-distance transport to new host areas. Spore escape is dependent on growth stage of the crop and the wind speed within the canopy (de Jong *et al.*, 2002). Warmer weather creates more and larger eddies of turbulent air that serve to mix spore clouds in the vertical direction (Arya, 1999). Spore clouds accordingly become deeper and more dilute as turbulent eddies of air lift spores upwards and away from the surface. This leads to a decrease in the surface deposition of spores, and thus a decrease in the risk of disease spread. Stronger winds serve to transport spores to new host areas at greater speeds. Survival of many types of pathogen propagules is dependent on the dose of solar radiation received (e.g. Mizubuti *et al.*, 2000; Wu *et al.*, 2002); therefore stronger winds and shorter travel times (or cloudier conditions) increase spore survival. With stronger winds there is less vertical mixing and spore deposition gradients flatten. Strong winds thus tend to increase the risk of substantial long-distance transport of viable spores. On days conducive to spore production, model results revealed that at 10 km from an inoculum source, there could be as much as four orders of magnitude difference in the number of viable spores depositing per metre downwind from the source, depending on atmospheric transport conditions (Skelsey *et al.*, 2009a,b,c). This type of aerobiological model, as a component in disease landscape simulators, together with downscaled climate variables generated by a GCM, can be adapted to investigate the potential influence of climate change on the spatiotemporal spread and management of epidemics.

Epidemic networks may be modelled based on host availability and other factors, such as the aerobiological process described above (Jeger *et al.*, 2007; Margosian *et al.*, 2009). Important properties of these networks may change under new climate scenarios, because of new geographic distributions of hosts and new geographic distributions of environmental conduciveness to disease, and thus conductivity.

5. Are there feedback loops for management?

It also is necessary to address the effect of disease management efficiencies within a context of global change (Coakley *et al.*, 1999; Chakraborty *et al.*, 2000). Nonlinearities and interactions must be expected, especially if multiple disease and pest systems are considered. Modelling approaches are key to address these, as, for example in wheat (Willocquet *et al.*, 2008). The effects of climate change can be exacerbated if there are feedback loops that make management less effective when pathogen populations increase. Feedback loops may occur when increases in disease make some types of management less efficient. Disease management that is based on reducing the amount of inoculum produced within a field is vulnerable to increased regional inoculum loads. For example, some types of disease resistance are based on reduced production of pathogen propagules per lesion. Within a field isolated from other sources of inoculum, this type of resistance will slow epidemics, because less inoculum would be produced for every pathogen generation. But in a field networked to other fields, in a landscape where a high level of inoculum transfer occurs, the beneficial within-field effect of this type of resistance may be reduced, possibly contributing to higher average regional disease intensity. Similarly, other methods that are based at least in part on controlling within-field inoculum production, such as field sanitation and many cases of intercropping and variety mixtures, may experience reduced efficacy when regional inoculum loads are high. And if higher disease pressure motivates more frequent pesticide use, this may increase the risk of pesticide-resistant pathogen populations.

Because plant disease severity and incidence often increase following a compound interest model, a small increase in the length of the growing season can have a large impact on inoculum load. This in turn may influence the viability of many forms of disease management. For example, the impact for disease reduction for potato mixtures with varying resistance levels decreased in regions where growing seasons were longer and thus there were presumably higher inoculum loads (Garrett *et al.*, 2009b). Potato late blight also illustrates two other related types of scenarios. First, as temperatures increase in the Andes (Seth *et al.*, 2010) the old strategy of using cooler highlands for susceptible varieties may disappear as farmers will eventually be limited by available lands or laws to protect vulnerable high-altitude ecosystems. Secondly, diseases like potato late blight may experience increases in risk when invasions of different mating types simultaneously change the probability of overwintering because of hardier sexual oospores (allowing epidemics to begin earlier in the season) and the probability of new genotypes with altered pathogenicity and environmental response types arising from sexual reproduction.

The potential for patterns of pathogen evolution to change under climate change is another important consideration (Chakraborty & Datta, 2003). The effects of resistance genes can vary with temperature. For example, many rice bacterial blight resistance genes have less effect at higher temperatures, whilst one gene studied was more effective at higher temperatures (Webb *et al.*, 2010). In tetraploid wheat, lines carrying *Yr36*, a previously unidentified stripe rust resistance gene from *Triticum turgidum* ssp. *dicoccoides*, are susceptible to almost all stripe rust races of *P. striiformis* tested at the seedling stage, but show adult-plant resistance to the prevalent races in California at high diurnal temperatures (Uauy *et al.*, 2005). Leaf and stem rust resistance is expressed differently as temperature increases (i.e. resistance does not work well at high temperature) (Singh & Huerta-Espino, 2003; Fetch, 2006). Where warmer summers are expected this could have unexpected effects on development of rust diseases, depending on whether very dry conditions make disease less likely or not. Durability of resistance is more complex in changing environmental conditions, although in general, the types of pathogen life history traits that confer more rapid adaptation to host resistance (McDonald & Linde, 2002) may also confer more rapid adaptation to climatic conditions. Of course, in some cases, new climatic conditions may be beyond the ability of pathogens to adequately adapt.

6. Are networks for intervention technologies slower than epidemic networks?

Many of the biggest problems for management will be in scenarios where farmers or policy makers have limited access to information about disease and disease management tools, and are confronted with a disease or pest that is new to them. Farmer knowledge of pathogens is often limited, compared to other system components, so intuition about how to respond to new pathogens is often limited too (e.g. Bentley, 1989). Responses to changes in agricultural risk factors will also need to be addressed at multiple spatial and temporal scales. The impact of increased risk factors will often be greatest for diseases or pests emerging from 'minor' to 'major' status, and for which farmers are challenged to develop new management methods in a short period of time. In the rice bowls of China and India alone, false smut, bakanae disease and spikelet rot are already achieving 'major' pest status as a result of recent emergence (Huang *et al.*, 2010a,b; Reddy *et al.*, 2010). In these cases, the demands on extension and information networks will be greatest, and inadequate links within these networks will be most apparent. This will be especially true in regions where farmers have fewer tools for accessing information independently. In coming decades, information resources for farmers will improve

dramatically if current development efforts are successful. However, wherever limitations to information and management options continue to exist, adaptation will be more challenging, and analyses of climate-change impacts will need to incorporate these limitations.

The threshold that allows farmers to recover from stress and shocks resulting from climate events and stresses is a function of the types of agricultural production situations, and their interaction with markets and the environment (Valdivia *et al.*, 2007). Interactions between climate, markets and changes in agriculture influence the ability of rural households to accumulate or deplete assets, and their ability to incorporate knowledge and invest resources in addressing this changing environment. This is a particular concern in the agriculture of developing countries, where risk-reducing institutions are currently limited or nonexistent. Until the necessary institutions are universally active, these issues will continue to be important. In the human realm, an important consideration will be how quickly new knowledge can be turned into practice, and, if knowledge is perfectible and constantly changing, identification of the types of human processes that allow new information to reach both the science and the decision maker.

As an example, in the present-day South American Altiplano there are varying degrees of access to and ability to use information (Gilles & Valdivia, 2009; Valdivia *et al.*, 2010). For some farmers, access to new information is rare, as often the networks of information are closed, meaning that information comes from family and friends (Gilles & Valdivia, 2009). Processes are needed that can expand these networks to include key stakeholders who have either power of knowledge, or formulating policies, which can in turn address the lack of access to information. It will be important to test different types of institutions and their effectiveness in sharing new information, but also in facilitating access to resources. Because problems with food insecurity occur where markets don't function well, analyses may need to consider 'partial market integration' and transaction costs. In other words, farmers may have difficulty accessing information, and the actual inputs they may need to act, and they may also have to migrate, reducing labour availability at home. Farmers, especially those with less labour, may learn about new IPM approaches, but may not have the time (labour) and resources to incorporate them. These practices often require that farmers act collectively in order to be effective, for example in keeping regional disease inoculum levels low.

Disease resistance is one of the most desirable forms of disease management for many reasons, but it also may have some problems for adoption by farmers. If disease occurrence is sporadic, it may be difficult for small-scale farmers to evaluate the benefits of using new resistant germplasm. Lybbert & Bell (2010) argue that drought tolerance may be less readily adopted by resource-poor farmers than Bt crops (crops engineered to produce the toxin from *Bacillus thuringiensis* for pest control) have been, because stochastic weather conditions will make the benefits of drought tolerance less apparent. Under conditions of either little drought or extreme drought, the benefits of drought tolerance will not be realized. The same may be true for adoption by farmers of crop varieties with many types of disease resistance, where the more common fluctuation between extreme conditions predicted in many climate scenarios may produce this type of problem for disease management. The usefulness of disease resistance may not be apparent when conditions do not favour disease, or when conditions are so disease-conducive that benefits from partial disease resistance are small. Ideally, systems such as farmer field schools will allow small-scale farmers to observe benefits of disease resistance in multiple environments in their associate's fields, in addition to their own (e.g. Ortiz *et al.*, 2004). Use of disease resistance may function analogously to insurance, as drought tolerance does (Lybbert & Bell, 2010), such that farmers pay for the resistance during times when disease conduciveness is low (or perhaps too high), but gain benefits when disease conduciveness is high.

7. Are there effects of plant disease on multiple ecosystem services?

Crop yield is often the most important ecosystem service, or benefit to humans, provided by agricultural plants, but many other benefits may also be gained or lost depending on plant disease pressure (Cheatham *et al.*, 2009). Management that decreases yield losses to plant disease, in itself, can be considered a contribution to the global carbon budget, because less land must be maintained in or converted to agriculture for the same level of food production (Berry *et al.*, 2008, 2010; Mahmuti *et al.*, 2009). In natural systems, plant disease may threaten natural plant diversity, as with the impact of *Phytophthora cinnamomi* in Australia (Cahill *et al.*, 2008). Likewise, wild crop relatives may be influenced by changes in disease intensities. As potato late blight moves into new territories, it has the potential to reduce diversity in wild potato species that were previously protected by low temperatures. Wild species may experience genetic bottlenecks or even extinction as a result of rapidly changing impacts from pathogen exposure.

One of the most important ecosystem services is maintenance of human health through availability of appropriate nutrients and minimized exposure to toxins and pesticides. The influence of cropping systems on human health can shift in at least four ways. First, reduced food productivity caused by plant disease may reduce food security through lower incomes for resource-poor farmers and food prices that may increase beyond the reach of human communities with little money. (Reduced food production from livestock may also result when livestock are fed grain contaminated with mycotoxins.) Secondly, disease pressures for increased pesticide use may increase exposure to pesticides in farmers and their families. This is a particular concern in regions where institutions to support safe pesticide use (such as education about and

enforcement of regulations) are not in place, and farmers routinely do not follow recommended practices for pesticide safety. Thirdly, higher disease levels may increase human consumption of mycotoxins and other unhealthy byproducts of plant disease. For example, elevated CO_2 levels may increase fungal biomass of *Fusarium pseudograminearum* (Melloy *et al.*, 2010), and thus also increase the potential for mycotoxin production. Fourthly, human pathogens may be more easily maintained in association with plants, especially under eutrophied conditions and reduced microbial diversity (Franz *et al.*, 2007, 2008; Klerks *et al.*, 2007).

8. Are there feedback loops from plant disease to climate change?

Ecosystem services that directly influence climate change deserve special emphasis in this framework. Epidemics may reduce ecosystem functioning with the potential to contribute to increased climate-change risk factors, such as when plant removal by pathogens results in reduced soil retention (Eviner & Likens, 2008; Cheatham *et al.*, 2009). This is in addition to the potential for an increased 'carbon cost' per agricultural product as a result of disease (Berry *et al.*, 2008; Mahmuti *et al.*, 2009). The 'carbon cost' can be in terms of yield loss and/or costs incurred through management of the disease. For example, management of *Phytophthora infestans* in northern Europe has been estimated at 3·0 GJ ha^{-1} energy (estimated as 12% of total production) and 224 kg ha^{-1} CO_2 emission (Haverkort *et al.*, 2009).

Applying the framework

The questions posed above to evaluate complexity can guide research prioritization, since answers are not available for all important systems. The same research will generally benefit current management strategies as well. Here we present an analysis based on the framework for two relatively well-studied diseases, fusarium head blight of cereals (FHB) and potato late blight (LB) (Table 2).

1. Both of these diseases affect multiple host species. Arthropod vectors are not considered important factors [although, interestingly, mite associations with some *Fusarium* species have been reported (e.g. Kemp *et al.*, 1996)]. In the case of FHB, different epidemic roles for different crop species mean that cropping systems influence disease risk, as one host species can provide a 'green bridge' when other host species are not available for the pathogen. For LB, host species such as tomato may support distinct subpopulations and thus have less influence on populations on potato, but in some regions abundant wild plant species may act as hosts. FHB also involves multiple pathogen species, so shifts in the composition of these pathogen communities have the potential to produce different epidemic outcomes. Thus, analyses of climate change impact on FHB may need to include information about global

Table 2 Examples of two pathosystems evaluated using the framework in Table 1. Entries include an evaluation of the level of complexity (++ = highly complex, + = somewhat complex, 0 = less complex)

	Fusarium head blight (FHB)	Potato late blight (LB)
1. Are multiple biological interactions important?	++ Multiple host species; multiple pathogen species	+ Multiple host species
2. Are there environmental thresholds for population responses?	0 Little evidence for this	0 Little evidence for this
3. Are there indirect effects of global change factors on disease development?	+ Land-use change: maize and wheat co-occurrence, and reduced tillage systems	+ Enhanced transportation networks: greater exchange of seed and pathogen populations
4. Are spatial components of epidemic processes affected by climate?	+ Temporal/phenological requirements for infection	+ Aerobiology/dispersal may be modified
5. Are there feedback loops for management?	++ Buildup of inoculum from multiple host species makes management more difficult	+ Worldwide, as sanitation and other techniques may become less useful ++ Highland tropics, as colder highlands disappear
6. Are networks for intervention technologies slower than epidemic networks?	+ Online risk evaluations available for some regions	++ Reliance on pesticides, with associated knowledge requirements; slower vegetative propagation of resistant varieties
7. Are there effects of plant disease on multiple ecosystem services?	++ FHB management may increase erosion and reduce support for wildlife; mycotoxins create health risks	+ Increased LB results in increased pesticide exposure for humans and environment
8. Are there feedback loops from plant disease to climate change?	+ Increased 'carbon cost' of wheat production; management with tillage may reduce carbon sequestration	+ Increased 'carbon cost' of potato production

change impacts on cropping systems and pathogen species interactions to be useful. Analyses for LB may need to include information about global change impacts on interactions among crop and wild plant pathogen populations.

2. Current understanding of FHB and LB does not suggest that there are important environmental thresholds. In other words, it is not known that the environment must support growth of populations of these pathogens to a certain threshold level before they can 'be released' to reproduce at a higher rate. (At larger scales, however, it is possible that there may be thresholds such that a certain level of infection must be reached in one region before dispersal to another region is likely.) Thus, at this point, there is no indication that climate-change effects on thresholds need to be included in analyses of FHB or LB.
3. For LB, increased movement of seed tubers and pathogen populations has contributed to increased epidemic risk in many parts of the world. Increased organic production of potato may also change epidemic landscapes. For FHB, changes in cropping systems, in terms of proximity of maize and wheat and increased use of reduced-tillage systems, influence epidemic risk. Thus, analyses of climate-change effects on LB may need to explore the impact of increased movement of populations globally, potentially providing a broader pathogen genetic base for adaptation to new conditions. Analyses of climate change effects on FHB may need to include climate-change impacts on shifts in cropping systems. For both systems, other socioeconomic factors that change cropping systems may need to be addressed.
4. For FHB, spatial components may be important, but phenological aspects are particularly relevant, because inoculum availability must be synchronous with host anthesis. For LB, climate change may impact the aerobiology of the pathosystem. Thus, analyses of climate change may need to include climate impacts on host and pathogen phenology, and climate impacts on dispersal, respectively.
5. For FHB, the buildup of local or regional inoculum impacts future disease risk, as residue from previous crops (wheat, barley or maize) can provide substrate for the pathogen to overwinter until the next cropping season (Dill-Macky & Jones, 2000). If maize produces more stover (stubble) under increased CO_2, this could result in higher rates of pathogen overwintering. Inoculum buildup can influence the efficacy of management for LB, for example by making use of sanitation or intercropping less effective. Higher elevation zones that are too cool for LB may cease to exist in some regions, removing the option of escape from disease. Thus, analyses of climate-change impacts may need to include increasing costs of management and decreasing effectiveness.
6. Intervention technologies are available for both FHB and LB, but not readily accessible by all farmers globally. FHB models have been developed and weather-based risk evaluations made available online for some regions (De Wolf *et al.*, 2003; http://www.wheatscab.psu.edu/). The importance of fungicide use for LB management makes its efficient management knowledge-intensive. Also, the spread of new LB-resistant potato cultivars is slower because of reliance on vegetative propagation. Thus, analyses of climate-change impacts for LB, particularly, may need to include models of farmer knowledge and decision-making processes, and the efficacy of intervention networks.
7. Both FHB and LB have the potential to strongly reduce ecosystem services, such as the production of food, and the efficiency of 'conversion' of natural resources into food. When FHB motivates the use of additional tillage, it increases the risk of soil erosion (Dill-Macky & Jones, 2000) and support of wildlife in farming areas (Rodgers, 2002). Additionally, FHB can reduce the quality of food produced, and thus the economic value for farmers and potentially the health of people and livestock who consume foods with mycotoxins produced by the pathogens (Snijders, 1990; McMullen *et al.*, 1997; Starkey *et al.*, 2007). The reliance on fungicides for LB management means that changes in LB risk will result in changes in fungicide exposure for farmers who do not follow appropriate safety practices, and changes in environmental fungicide loads. Thus, analyses of climate-change impacts related to both these diseases may need to include these additional impacts beyond simple changes in crop yield.
8. Both FHB and LB can sharply reduce crop yield, increasing the 'carbon cost' of food production. Management of FHB using tillage may reduce carbon sequestration. Full analyses of climate-change mitigation may be improved by incorporating the cumulative global impacts of diseases such as these.

Discussion

Approaches for scaling models of epidemiological processes remain an open area for research. Epidemic interactions may be modelled across larger spatial scales using a 'disease neighbourhood' approach (Willocquet & Savary, 2004). Whilst most models of larger-scale disease risk are based on a point-by-point analysis of risk factors, new models may improve predictions by incorporating the effect of risk levels in neighbouring regions (AH Sparks, GA Forbes, RJ Hijmans, KA Garrett, unpublished data), including network models of plant disease epidemics (Jeger *et al.*, 2007; Margosian *et al.*, 2009). A quantitative understanding of emerging properties during scale transitions is still in its infancy (Gilligan *et al.*, 2007; Cunniffe & Gilligan, 2008). Although patterns of disease spread in foci hint at self-similarity of processes at different scales (e.g. Zadoks & van den Bosch, 1994), this has not been investigated quantitatively in relation to climate-change scenarios on large scales. The integration of various temporal and spatial scales of weather patterns and their effects on disease development will need to be

studied, taking generation time and dispersal capacity into account, in order to understand the invasion of a pathogen in hitherto unoccupied space.

The response of a pathogen to a variable climate and other environmental conditions is difficult to predict unless the probabilities of those conditions and the probabilities of pathogen population shifts are taken into account. Probabilistic risk models have been developed for various human pathogens (Franz *et al.*, 2007, 2008), but these models are still relatively rare in plant pathology (De Wolf *et al.*, 2003). Yet, probabilistic models are urgently needed to anticipate changes in epidemic development of existing pathogens and the potential invasions by emerging pathogens. The current and potential variation within species of pathogens needs to be taken into account as well, in order to predict evolution of subpopulations of pathogens.

Discussion of complexity naturally leads to the concept of complex adaptive systems. These can be defined as systems in which 'higher-level' patterns emerge as a result of interactions and processes at lower levels (Levin, 2005). More formally, a complex adaptive system may be said to have three traits (Levin, 2005). First, it includes 'sustained diversity and individuality of components'. Secondly, it exhibits 'localized interactions among those components'. Thirdly, it is 'an autonomous process that selects from among those components, based on the results of local interactions, a subset for replication or enhancement'. These three characteristics will tend to hold for pathogen populations and microbial communities in general, which continually change in structure in response to selection pressures. A complex adaptive system may be resilient if it tends to maintain its higher-level traits despite changes at lower levels; this may result from system redundancy, such as when multiple microbial taxa may play similar functional roles, or when multiple plant species can satisfy people's needs for ecosystem services. To the extent that a system such as an agricultural system is in a desirable state, resilience will be desirable. Levin (2005) also discusses the role of system heterogeneity in supporting resilience, suggesting that agricultural systems are not complex adaptive systems, strictly speaking, because their simplified structures are determined exogenously rather than developing endogenously, leaving them highly vulnerable to problems such as diseases. To strengthen resilience, it is necessary to understand how resilience 'emerges' from processes at lower levels.

The concept of complex adaptive systems has been applied for analysis of agricultural systems in the context of *Cassava mosaic virus* in the Soroti district of Uganda (Hall & Clark, 2010). Farmers and consumers in this area had been dependent on use of cassava, but cassava production was no longer feasible in many areas after this disease became common. The system did adapt, to a degree, through use of sweet potato as a substitute for cassava, although this was generally perceived as a less satisfactory resulting system.

As Green *et al.* (2005) show in their review, ecological modelling has tended to focus on testing a particular hypothesis rather than comparing a potentially large set of alternative models. Thus, researchers considering what level of complexity is necessary for a model predicting climate-change impacts on plant disease, or on effects mediated by plant disease, will generally not have a familiar set of tools for deciding among models, although new tools are being implemented (Burnham & Anderson, 2010). Green *et al.* (2005) recommend developing a set of related models at different scales and levels of complexity as a step in understanding the mechanisms that produce patterns at higher levels. In the context of our set of questions related to system complexity, development and exploration of model predictions with and without inclusion of factors identified here can be used to evaluate the sensitivity of model outcomes to each relevant factor.

Multiple models – perhaps those designed to optimize precision, realism and generality – can be used simultaneously, to improve confidence in predictions when the predictions are similar and to reveal the potential need for more information when predictions diverge. In practice, two long-term phases of model development may be necessary. In the first phase, additional research will be used to parameterize larger and more detailed models. In the second phase, the larger models will be evaluated to determine which model components are less important and can be removed from models to support policy and prioritization. Complex climate-change scenarios challenge international institutions and legal frameworks (Deere-Birkbeck, 2009). The scale and type of policies necessary for natural resource management may vary widely from one setting to another, calling for adaptive management approaches (Ostrom, 2007; Ostrom *et al.*, 2007). Other potential types of complexity that we have not addressed include legacy effects and time lags in responses to new scenarios (Liu *et al.*, 2007a,b). Farmers who are resource-poor and economically vulnerable, with weak safety nets, are unlikely to take new risks. Participatory processes to incorporate new knowledge in decision-making under uncertainty, and policies that address the lack of safety nets, are preconditions to enable decision makers to explore alternative strategies or practices in vulnerable regions (Davidson, 2010; Valdivia *et al.*, 2010). Whilst the structural complexity of social and ecological systems is similar, they differ in the nature of their feedback processes (Davidson, 2010). Individual organism's responses are not defined only by structures, but also by agency. Change in social systems through human agency may lead to adaptation, resilience or transformation (Davidson, 2010).

New models, as well as new frameworks for thinking and ensuring research impact, are needed to address changes in agricultural risk factors resulting from climate change. Important components of these models will be factors to address biological complexity, such as the incorporation of thresholds, interactions and feedback loops. These forms of biological complexity will need to

be 'scaled up' in models such as those that incorporate 'risk neighbourhoods'. Finally, models with these forms of biological complexity will need to be linked with models of information networks and market influences to predict where new demands will be placed on research, extension and education systems.

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