A metamodeling framework for extending the application domain of process-based ecological models

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Abstract. Process-based ecological models used to assess organisms' responses to environmental conditions often need input data at a high temporal resolution, e.g., hourly or daily weather data. Such input data may not be available at a high spatial resolution for large areas, limiting opportunities to use such models. Here we present a metamodeling framework to develop reduced form ecological models that use lower resolution input data than the original process models. We used generalized additive models to create metamodels for an existing model that uses hourly data to predict risk of potato late blight, caused by the plant pathogen *Phytophthora infestans*. The metamodels used daily or monthly weather data, and their predictions maintained the key features of the original model. This approach can be applied to other complex models, allowing them to be used more widely.

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INTRODUCTION

There is growing interest in process-based modeling approaches to study the distribution of species (Chuine and Beaubien 2001, Kearney and Porter 2004, Morin et al. 2007, Jackson et al. 2009, Monahan 2009, Buckley et al. 2010), but data requirements for both model development and application have limited the types of questions that can be addressed with these approaches. There is also increasing interest in using such models for strategic assessments of the value of new management practices (Hijmans et al. 2003) and responses to climate change (Rosenzweig and Parry 1994, Hijmans 2003, Audsley et al. 2008, Luedeling et al. 2009).

However, modeling the distribution of species over larger areas is dominated by correlative approaches (Guisan and Thuiller 2005, Elith and Leathwick 2009). This is in part because of the absence of process-based models for many species, but also because the large extent - high resolution data sets needed to apply such models often are not available.

Process-based ecological models typically require high temporal resolution weather data (e.g., daily or hourly data). This is particularly true for process-based models that capture, for example, the short generation times of microbial and arthropod populations and communities (Fry et al. 1983, 2004, De Wolf et al. 2002, Grünwald et al. 2002, Scherm and van Bruggen

1994). Even for plants and animals with long generation times, many ecophysiological processes occur at short time scales (e.g., an extreme frost event; Hijmans et al. 2003). Process-based models have been used, for example, to study the growth and development of crops (De Wit and Brouwer 1971) and crop disease (Van der Plank 1963), to simulate greenhouse gas emissions from soil (Li et al. 1992, Giltrap et al. 2010), and to predict the spatial distribution of species (Kearney and Porter 2004). The need for high temporal resolution input data can make it very cumbersome, or impossible, to use such models over large spatial extents (Fig. 1; Morin and Lechowicz 2008, Thuiller et al. 2008, Randin et al. 2009). Here we develop an approach for adapting models that were developed using input data with high temporal resolution, so that they can be used with lower resolution input data.

There have been two main approaches for applying models across large areas for which high temporal resolution data are not available: (1) The model is applied for locations where sufficient data are available (e.g., a limited number of weather stations supplying daily weather data) with predictions interpolated between these locations/times (De Wolf et al. 2002, Wu et al. 2006). (2) Higher resolution input data are generated from lower resolution input data; for example, small time-step weather such as rainfall patterns can be generated from larger time-step data through stochastic weather generators (e.g., Wilks and Wilby 1999, Hijmans et al. 2000). Both of these approaches have drawbacks. Interpolation between stations that are far apart may not adequately capture the non-linear effect of weather on the model organism. Stochastic simulation of weather data is complicated and computationally intensive, and the response model needs to be run many (e.g., 100) times to obtain an average response. Here we develop an alternative approach, (3) the use of metamodels, adapting a model so that it can be used with lower resolution input data. The term metamodel can refer to a simplification of the original model that retains its salient features, or to a single model created by combining the results of multiple models. In this paper we present a metamodeling framework to extend the application domain of a model, so that the metamodel can be applied to lower temporal

resolution weather or climate data. Metamodels have been developed in bio-economics (Lakshminarayan et al. 1996, Breukers et al. 2007, Kristensen et al. 2008), and in manufacturing industries to improve design optimization (Wang and Shan 2007). In ecology they have been used to organize and synthesize models (Slobodkin 1958), to facilitate the study of endangered species risk assessments (Nyhus et al. 2007), and to assess impacts of socio-economic and climate change on wetlands (Harrison et al. 2008). Lastly, in ground water management metamodels have been used as a way to reduce model complexity while keeping those processes and parameters for which the simulation output is sensitive, or for which input data are available (Tiktak et al. 2006). Many metamodels have been constructed to consolidate different models into a single model, but to our knowledge they have not been used in ecology to extend the application domain of the original model as we do here.

Our framework for metamodel development consists of the following steps (Fig. 2). (1) A well-validated initial process-based model is available that would be desirable to use, but its application is limited to high resolution input data. (2) A large, high resolution, input data set is selected to match the requirements of the initial model, and to be representative of the types of conditions in which we would like to apply the resulting metamodel. (3) The initial model is applied to generate predictions from the input data set. (4) A second set of input data is generated by averaging to the level of aggregation at which such data are more generally available. (5) If predictions from the initial model are higher resolution than output from the new metamodel will be, a second set of predictions is generated by averaging the high resolution predictions to the desired level of aggregation. (6) The aggregated data of step 4 (and step 5 as needed) are divided into model construction and evaluation sets. (7) The metamodel is constructed to describe the relationship between the aggregated input data and aggregated predictions from the initial model. (8) The metamodel performance is evaluated for the evaluation data set. (9) The metamodel is evaluated in terms of potential limitations, in general and in comparison to the initial process-based model.

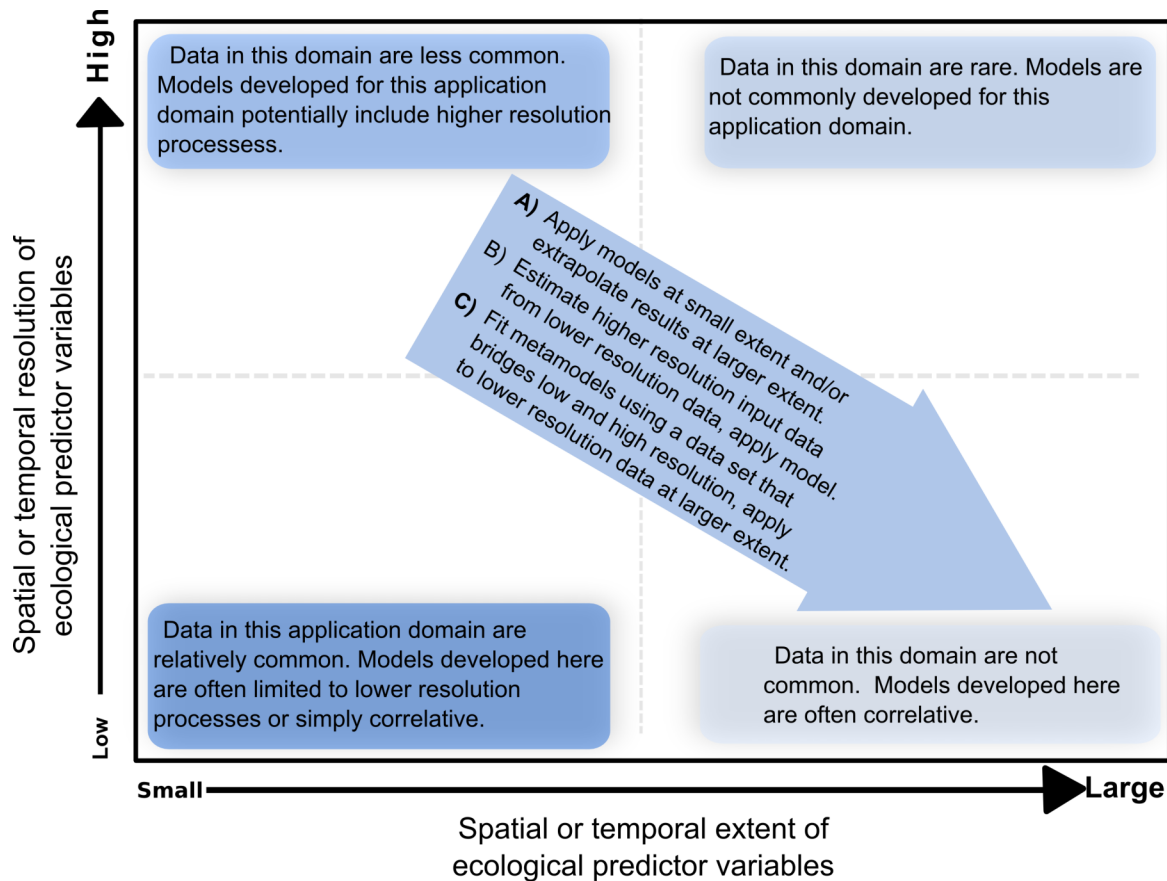We used potato late blight disease (caused by

Fig. 1. Ecological modeling has most commonly been based on data from a small spatial or temporal extent and low level of spatial or temporal resolution. When higher resolution data are available, this often makes it possible to develop process-based models, even for high resolution processes such as microbial and arthropod community interactions and ecophysiological processes. Such models can be used, in turn, to create metamodels that do not require as high a level of resolution for input data, and can thus potentially be applied across greater extents.

Phytophthora infestans (Mont.) De Bary., the proximate cause of the Irish potato famine) as a model system for application of this framework because it is well-studied, with well-validated high resolution models available, and its ecology illustrates the type of sensitivity to high resolution variation in weather that is common to many microbes and arthropods. Late blight forecasting models recognize the importance of temperature and moisture in disease development, and have evolved over time using combinations of these variables for forecasting. The earliest of these models for predicting late blight risk were the "Dutch Rules" postulated by Van Everdingen (1926, and discussed in Beaumont (1947)). Fry et al. (1983) developed SimCast, a predictive late

blight model designed for analysis of economic timing of pesticide applications, which included the effect of potato genetic resistance to disease. Grünwald et al. (2002) further refined the SimCast model for potato genotypes with moderate to high disease resistance and demonstrated that it performed well in a tropical highland climate, even though it was originally developed in a temperate climate. The SimCast algorithm is based on counting the hours during a day (from noon to noon the next day because the period of high relative humidity occurs overnight) when relative humidity (RH) is above 90% (a proxy for the presence of leaf surface moisture (Kim et al. 2010)). The number of 'blight units', a measure of disease risk, is computed based on the number of

Preparation for Data Aggregation and Metamodel Development

1. Select initial model

We used SimCast, a process-based model for potato late blight that uses input weather data with hourly resolution.

2. Select high resolution data

The data should match the initial model's application domain. We used the HUSWO dataset which could be aggregated to match the desired application domain.

3. Generate initial model predictions

Initial model predictions based on high resolution data are used to construct the metamodel.

4. Aggregate high resolution data

High resolution data are aggregated into the desired format. We aggregated hourly weather data into daily and monthly, as predictors for the metamodel. Aggregation must match aggregation of the initial model results.

5. Aggregate initial model results

The initial model results are aggregated into the desired format, e.g., hourly to daily, or daily to monthly. This aggregation must match the aggregation level of the high resolution data.

6. Create construction and evaluation subsets of aggregated data

We split the data sets by year, the training data set 1990-1992, the testing data set 1993-1995.

Metamodel Development

7. Construct metamodel

We used the construction subset of aggregated data to construct GAMs which used daily and monthly weather data.

8. Test metamodel

We used the evaluation subset of aggregated data to test the model's performance.

9. Evaluate metamodel's limitations

The late blight metamodel retained the correct relative values for output, but tended to produce underestimates

Metamodel Implementation

10. Prepare new low resolution input data of interest

We are using the late blight metamodel to evaluate risk for input data sets with monthly resolution.

11. Apply metamodel

12. Interpret metamodel's performance

The late blight metamodels give useful relative values but underestimate absolute values.
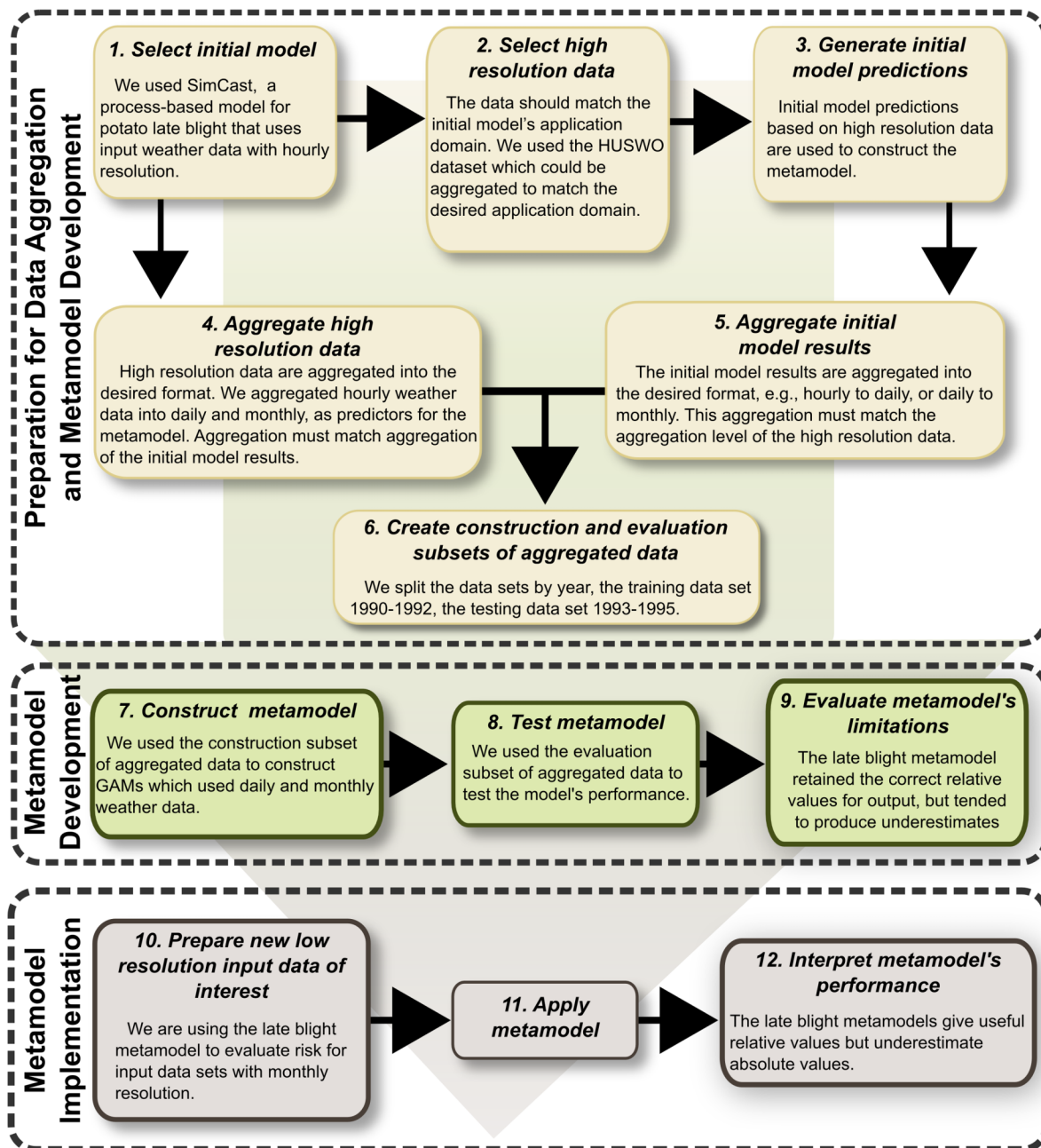
Fig. 2. Steps in metamodel development. A suitable initial model which predicts desired output is chosen. Then data are obtained which match the initial model's application domain and are flexible enough to be adapted to new model application domains, and are also representative of the future data sets for analysis. The initial model is applied to the unmodified data. Then the initial data and initial model predictions are aggregated in order to construct the metamodel, which is applied to lower resolution input data. Once the metamodel has been constructed, evaluated, and its limitations determined, it can be applied to a new lower resolution dataset.

consecutive hours over 90% RH, the temperature (T) during those intervals, and genotype-specific

host resistance to disease. SimCast is typical of models for foliar disease, capturing an important

aspect of the infection process: periods of moisture must occur, at disease-conducive temperatures that last long enough to support foliar infection. Hijmans et al. (2000) used these types of models at a global scale to estimate the number of pesticide applications necessary to manage late blight, using monthly climate data and a weather generator (approach 2 described above) for dealing with low resolution weather data. Because SimCast has become well-established as a successful tool for late blight management and research (Skelsey et al. 2009) in many areas of the world, we used it for development of potato late blight metamodels.

Our overall goal in this study was to provide a framework for constructing metamodels that can readily be applied to scaling ecological models, thereby extending their application domain from high resolution input data to low resolution input data, and thus supporting their application across large extents. We developed a metamodel of the SimCast potato late blight risk model. Our primary objective was to develop disease risk models that use monthly or daily weather data as input, and compare the predictions made with these models to predictions made with the initial model that uses hourly weather data. This type of application domain extension has many potential applications for scenario analysis for potato late blight, specifically, and as an example of the potential for scaling other models. A secondary objective was to compare the performance of models constructed using targeted weather data from regions where the host of the disease occurs, with the performance of models constructed using a data set that represents a broader range of climates. As indicated under step 2 of the framework described above, the data set used for metamodel construction should be representative of intended application scenarios for the model, but it is an open question whether the targeted or broad approach is best.

METHODS

Our first objective was to develop disease risk metamodels for use with temporally aggregated weather data and compare the performance of these models with the original model that uses high resolution input data. As step (1) in the metamodeling framework (Fig. 2), we had

identified SimCast as a model that has been well-validated in a number of environments, but requires hourly temperature and relative humidity data as input. (2) We needed a data set with wide geographic coverage, hourly reporting, and extensive data quality control. The National Climatic Data Center Hourly United States Weather Observations (HUSWO) 1990–1995 meet these criteria (US-EPA and NOAA 1997), containing hourly weather observations from 262 National Weather Service stations nationwide. Data from the 247 stations reporting hourly temperature, relative humidity, and precipitation were included in the analysis. Weather data from the US represent all five of the main groups of the Köppen-Geiger climate classification system, and 22 of 31 climate classes (Kottek et al. 2006, Rubel and Kottek 2010); classes not represented are unlikely to support potato production. HUSWO data were split into two subsets for model construction (1990–1992) and model evaluation (1993–1995). (3) Blight units for each day at each location in the HUSWO data set were predicted for susceptible and resistant genotypes using SimCast as presented in Grünwald et al. (2002). These 'true' blight units based on predictions from hourly input would then be used as the standard for analysis of the metamodels. (4) We were interested in comparing metamodels for both daily and monthly resolution. The HUSWO data were averaged (within each location) to provide day-resolution and month-resolution aggregated input data. So, for example, each HUSWO location-year supplied 12 months of month-resolution data and 365 or 366 days of day-resolution data. It could be argued that consecutive days and adjacent locations are not statistically independent because of autocorrelation in weather patterns, but the large size of this data set makes lack of strict independence unimportant. (5) SimCast takes hour-resolution input data and produces day-resolution predictions, so 'true' day-resolution blight units were generated without the need for any aggregation step. To produce 'true' month-resolution blight units, the 'true' day-resolution blight units were aggregated.

(6–7) We selected generalized additive models (GAM) (Hastie and Tibshirani 1986) as an example of a flexible modeling approach for constructing the metamodels, allowing us to

directly compare the performance of simpler and more complex models. The form of SimCast (Grünwald et al. 2002) suggested a simple linear model would not be sufficient. We developed and tested GAMs to model the relationship between aggregated weather data and aggregated 'true' blight units (Table 1). The first GAM metamodel had the form of a simple linear model for the sake of comparison, with blight units (BU_i) as the response variable, and temperature (T_i) and relative humidity (RH_i) as predictor variables, where i indicates the ith location-day (or location-month) in the HUSWO data set for the model construction interval 1990–1992. The second general form of GAM metamodel again had T_i and RH_i as predictor variables, but used the penalized regression spline smoothed function of their interaction, with k as the dimension of the basis used to represent the smoothing term (Wood 2006). Daily and monthly resolutions were evaluated for both susceptible and resistant potato genotypes. The metamodels were constructed in the R environment (R Development Core Team 2010) using the contributed package MGCV (Wood 2008). In the rare cases when blight unit values were predicted to be less than zero, they were set equal to zero. Models were evaluated based on their Generalized Cross Validation (GCV) scores, AIC (Akaike Information Criterion (Akaike 1974)), and R-squared values.

(8) The metamodel was then evaluated with the evaluation data subset from the years 1993–1995. We compared Pearson's correlation coefficients for the SimCast predicted values and the metamodel predicted values (Table 2). The daily metamodel (mm_{Daily}) predictions could be compared directly, but to compare with the monthly metamodel ($mm_{Monthly}$) outputs, SimCast blight unit predictions were averaged, creating an average of daily blight unit accumulation per month.

The secondary objective was to compare the performance of models constructed using weather data sets specific to host regions, areas where potato is grown within the US, with models constructed using a data set that represents a broader range of climates. Data from Hijmans (2001) were used to determine which of the HUSWO station locations were within potato growing regions in the US. Weather stations in the potato growing areas or within a distance of 10 kilometers were selected and a subset of weather data from these stations was created for use in metamodel construction as detailed in objective one.

RESULTS

Metamodel construction and fit

The models that considered an interaction of temperature and relative humidity yielded lower AIC and GCV scores than the model that did not (Table 1), indicating better fit. For mm_{Daily} a k value of 100 was selected (Fig. 3). As k increased to 150, the time to run the model increased and the gains in fit were small (Model 2d; Table 1). For $mm_{Monthly}$ $k = 150$ was selected (Fig. 3). When $k = 200$, $mm_{Monthly}$ begins to decrease in performance with higher GCV and AIC values (Model 2f; Table 1). The resulting GAM surfaces

Table 1. Performance of metamodels. In the generalized additive model (GAM) equations, BU is blight units, T is temperature, RH is relative humidity, s indicates that the interaction of the variables is smoothed, and k is the dimension of the basis used to represent the smooth term. P-values are all <0.01 and <0.001 for mm_{Daily} and $mm_{Monthly}$, respectively.

Model	GAM	mm_{Daily} (susceptible)			$mm_{Monthly}$ (susceptible)		
		R^2	GCV†	AIC†	R^2	GCV†	AIC†
1	BU = T + RH	0.26	3.2981	954,010	0.43	0.61753	18,314
2a	BU = s(T, RH, k = 50)	0.61	1.7493	803,934	0.78	0.24147	11,015
2b	BU = s(T, RH, k = 100)	0.62	1.7153	799,296	0.78	0.23813	10,906
2c	BU = s(T, RH, k = 150)	0.62	1.7040	797,733	0.78	0.23694	10,867
2d	BU = s(T, RH, k = 200)	...	...	...	0.78	0.27300	10,878
2e	BU = s(RH, T, k = 100)	0.62	1.7144	799,175	0.78	0.23777	10,894
2f	BU = s(RH, T, k = 150)	...	...	...	0.78	0.23717	10,874

†Generalized Cross Validation (GCV) score, and Akaike's Information Criterion (AIC) were used in model selection, where a lower score indicates a better model fit.

Table 2. Goodness of fit and Pearson's Correlation scores of mm_{Daily} and $mm_{Monthly}$ metamodels when fit to SimCast-predicted blight units for construction (Con.) and evaluation (Evn.) datasets for complete US weather data and construction datasets based only on potato producing areas of the US. The SimCast model uses hourly weather data to predict blight units based on hourly weather data. The mm_{Daily} and $mm_{Monthly}$ metamodels predict blight units based on daily and monthly time-step weather data, respectively.

	mm_{Daily}				$mm_{Monthly}$			
Region	R^2	p	Con.	Evn.	R^2	p	Con.	Evn.
All US (Susceptible)	0.62	<0.001	0.85	0.84	0.78	<0.001	0.89	0.89
US potato regions (Susceptible)	0.62	<0.001	0.76	0.74	0.83	<0.001	0.91	0.91
All US (Resistant)	0.65	<0.001	0.81	0.81	0.76	<0.001	0.88	0.88
US potato regions (Resistant)	0.66	<0.001	0.82	0.82	0.83	<0.001	0.91	0.90

indicate the type of interaction between temperature and relative humidity for predicting the accumulated blight units (Fig. 3) that might reasonably be expected based on the structure of SimCast (Grünwald et al. 2002). Once the metamodel forms were selected, metamodels for resistant genotypes were also constructed using these forms of GAM for mm_{Daily} resistant and $mm_{Monthly}$ resistant (Fig. 3).

SimCast versus mm_{Daily} and $mm_{Monthly}$ metamodels

Metamodel predictions for both model construction and model evaluation data sets were similar to the results obtained with the original SimCast model (Fig. 4). mm_{Daily} had Pearson's correlation scores of 0.85, 0.84 for construction and evaluation data sets, respectively. The correlation scores for $mm_{Monthly}$ for construction and evaluation data sets were both 0.89. The number of accumulated blight units per day was underpredicted by both mm_{Daily} and $mm_{Monthly}$ but predictions by the latter were closer to the SimCast predicted averages (Table 2). While there were large differences between the model predictions, the metamodels successfully captured the main trends and rankings predicted by SimCast (Fig. 4).

The structure of SimCast (Grünwald et al. 2002) causes the accumulation of six or seven blight units per day to occur less frequently than other blight unit values. The weather conditions required for these values to register are ideal for late blight development; seven blight units requires 13–24 hours of a temperature at 13–22°C with the relative humidity above 90%. This is not a problem for SimCast's typical applications, but it does mean that there were relatively

fewer observations for fitting the GAM at six and seven blight units, and the model exhibits slightly different behavior for these values (Fig. 4) for a susceptible genotype.

Comparison when using potato growing areas only to construct GAM

The metamodels showed little difference in performance when created from the whole US weather data set or data sets constructed from potato growing regions of the US. Both metamodels under predicted blight units when compared to blight units predicted by SimCast, although again, the $mm_{Monthly}$ metamodel predictions were closer. However, both metamodels maintain a high correlation with SimCast blight units (Table 2). Similarly the application of a model created using the whole US data set when applied to just potato growing regions showed little difference from a model created using the whole US data set and applied to the whole US. Goodness-of-fit values were similar for all combinations tested (Table 2).

DISCUSSION

We used a metamodel framework to create a new model based on an ecological model that needs high temporal resolution input data, so that it can be applied with low temporal resolution input data that may be available at a relatively high spatial resolution over large extents. In the discussion we focus on the different steps of the metamodel framework (Fig. 2) in relation to the potato late blight model and more generally for other ecological models.

(1) There is potential for metamodel construction for a wide range of mechanistic models.
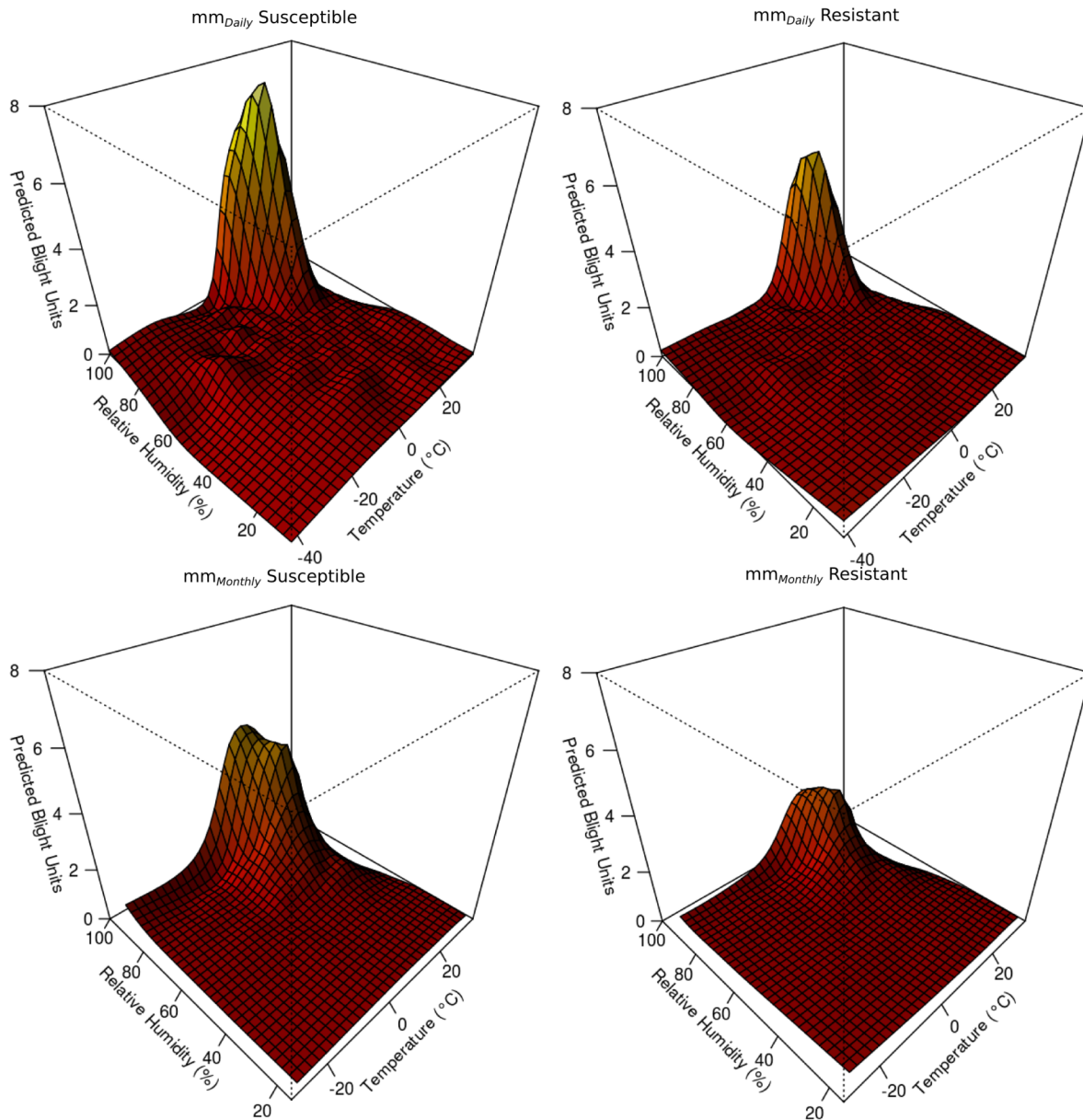
Fig. 3. Generalized additive model surfaces depicting mm_{Daily} and $mm_{Monthly}$ predicted blight units as a function of the interaction of relative humidity (%), and temperature (°C), for susceptible and resistant potato genotypes.

Models for many plant diseases are similar to the late blight model in that they use weather thresholds which, when crossed for defined brief time periods, trigger a predicted increase in disease risk in the model (e.g., Cu and Phipps 1993, Momol and Aldwinckle 2000). For other diseases, inputs related to phenology of the host plant, soil texture, inoculum, sowing density and nitrogen may be needed in addition to climatic variables (De Wolf and Isard 2007, Ennaïfar et al. 2007). Coupled energy and mass balance equations describing organisms and their habitats in biophysical models (Kearney and Porter 2009) may also be amenable to this approach, as well as
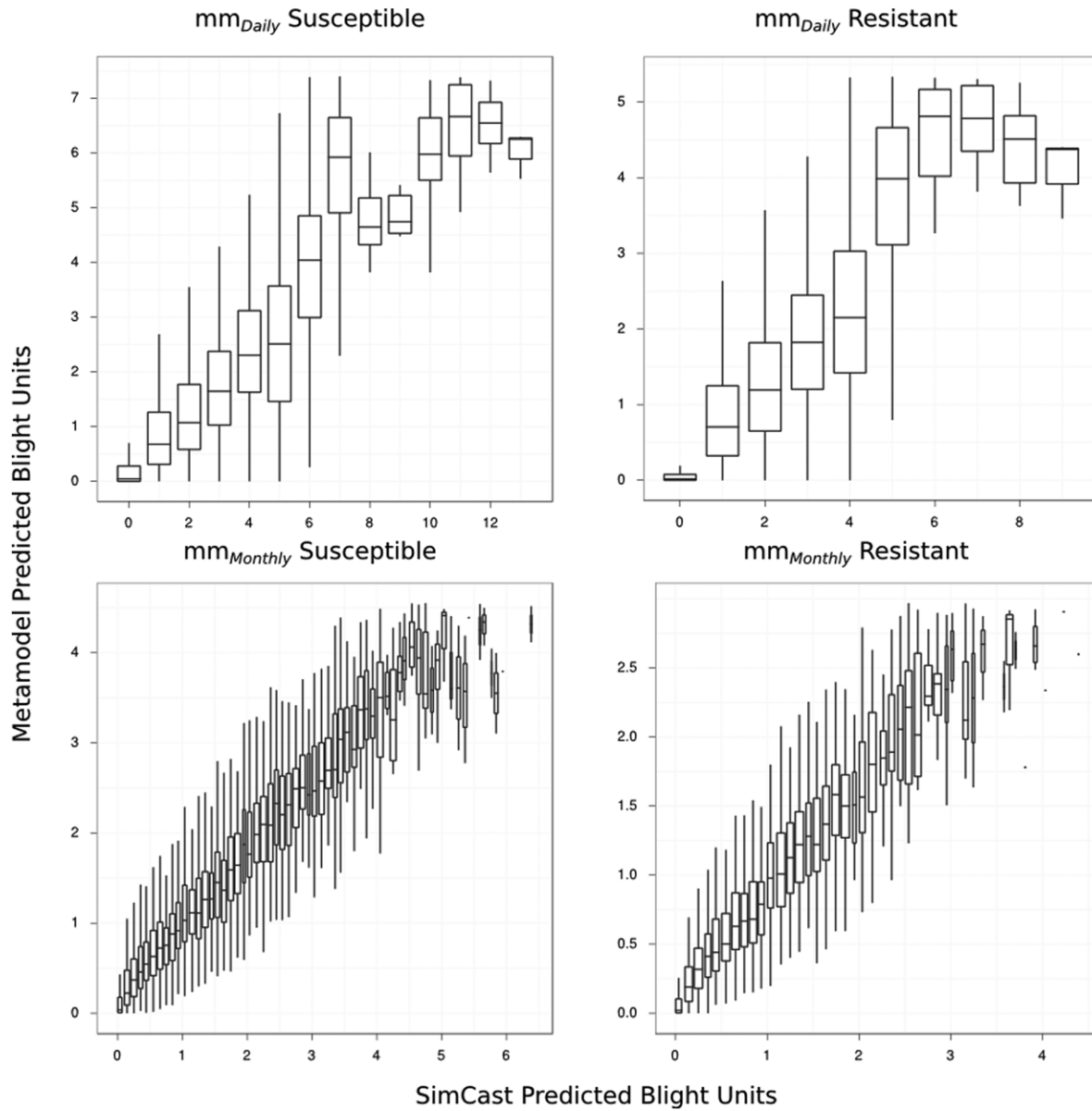
Fig. 4. Boxplots depicting mm_{Daily} and $mm_{Monthly}$ predicted blight units using evaluation data sets plotted with SimCast predicted blight units per day and the monthly average of SimCast predicted blight units per day, respectively, displayed by 0.1 blight unit bins for susceptible and resistant potato genotypes.

models that are based on limiting factors for survival, such as components of PHENOFIT (Chuine and Beaubien 2001) and CLIMEX (Sutherst and Maywald 1985), depending on their response to extreme input values.

The sensitivity of the initial model to extreme input values, in combination with the tendency or lack thereof for extreme input values to influence aggregated input values, will be an important determinant of the success of meta-modeling. Initial models may also be sensitive to the high resolution covariance structure of different input variables; again, the importance of this sensitivity will depend in part on how high resolution covariance translates to covariance in averaged input data. Because SimCast

includes a threshold RH value for infection to occur, it is sensitive to extreme values, and to the interaction between RH and temperature. However, enough of the high resolution features were maintained in the average values that the ordering, though not the absolute values, of the initial model output were maintained in the metamodel output.

(2) The high resolution data used for metamodel construction need to have several characteristics. The data need to match the initial model's application domain, in the case of SimCast having weather data available with hourly resolution. The data need to be such that they can be modified to match new desired application domains. This can generally be accomplished through data aggregation, in the case of SimCast by aggregating the hourly data to produce daily and monthly means. The data need to be extensive enough to provide good coverage of existing variation in weather patterns. In our case, the fit of potato late blight metamodels developed using a broad data set (all the US weather data) or a targeted data set (only those from potato-growing regions) were essentially the same. We chose to use the models constructed using the whole US weather data set. This approach represented a broader range of climates and was thus potentially more suitable for global predictions. In fact, the HUSWO weather data set may be equally useful for many ecological models that need to be adapted from requiring high resolution weather data input to lower resolution input data. The HUSWO data are extensive enough that, in our system, the fit of models for the evaluation subset of the data was essentially the same as for the construction subset. Finding large higher resolution input data sets for other types of predictor variables may be more challenging. In such cases, simulated input data (e.g., from a stochastic weather generator) could perhaps be used for construction of the metamodel.

(3–5) The degree to which data can be aggregated for model input is dependent on the system being modeled. Because potato grows over a period of months and is grown in many areas of the world at different times of the year, and late blight is polycyclic, it is most practical to aggregate data to the monthly level. The appropriate level of aggregation remains to be deter-

mined for other systems such as plant diseases with a narrow window of infection, including fireblight, where blossom infection occurs within a two to four day window (Thomson 2000) or Fusarium head blight of wheat and barley, where infection only occurs during anthesis (De Wolf et al. 2002). If the key input values for determining the response are in a tail of the distribution of input values, the effect may not be preserved. In our case, mm_{Daily} and $mm_{Monthly}$ maintain relative relationships. If a true one-to-one relationship between the original model and metamodel is necessary, the key input values would need to be conserved through averaging.

(6–7) For construction of the metamodel, we used GAMs to model the relationship between the aggregated initial model output and the aggregated weather data input. GAMs have the benefit of flexibility for fitting potentially irregular surfaces resulting from complex ecological interactions. Because they capture irregular surfaces well, their use puts additional emphasis on the requirement that the data set used for metamodel construction be large and representative. Other smoothing functions could also be used, and for simpler models low order polynomial models may be sufficient. In our case, simpler versions of the GAM model that did not include the interaction between temperature and RH performed poorly. In some cases, a priori model structures may be used. It can be argued that use of smoothing functions results in a metamodel that is once more, in some sense 'correlative'. However, the metamodel incorporates much of the complex information embedded in the structure of the process-based initial model, which will tend to provide advantages over approaches such as climate matching.

(8–9) Evaluation of the metamodel has the potential for several stages. Ideally the initial model will be well-validated over at least a small extent, so that similarity of metamodel predictions to initial model predictions is a good measure of how well the metamodel performs. A second form of evaluation, again assuming the reliability of the initial model, is similarity in results for metamodel application to the construction vs, the evaluation datasets, as we observed for potato late blight. For metamodels constructed from less-studied initial models, other forms of evaluation will be particularly

important. It would be ideal to have 'response' data corresponding to the high resolution input 'predictor' data used to construct the metamodel across a large spatial or temporal extent, but that scenario will be rare. At least it may be possible to evaluate the performance of the new meta-model for a limited number of observations.

The metamodel will tend to have all the limitations of the initial model, other than the requirement for higher resolution input data, and may have additional limitations, as well (though it may be less sensitive to outliers). In the case of potato late blight, SimCast provides an estimate of daily disease risk, but does not incorporate factors such as the potential 'compound interest' buildup of pathogen populations through the season (e.g., Garrett et al. 2009, 2011). There is also the potential for pathogen populations to evolve such that temperature optima shift, or so that resistance to the pathogen population is less effective. Thus, the metamodel shares these limitations. The metamodel construction frame-work performed well for scaling the model of disease risk based on hourly weather input to metamodels using daily or monthly average weather inputs. Predictions from both the daily and monthly resolution metamodels were strongly and positively correlated with predictions from the original hourly resolution SimCast model (Table 2). The salient features of SimCast were maintained in the metamodels, even though the relationship was not one to one. A limitation of this metamodel is that, although it preserves relative changes in disease risk, it does not preserve absolute changes. Interestingly, the fit of $mm_{Monthly}$ when regressed on SimCast output was slightly better than that of mm_{Daily}. Reasons for this may include the smoothing effect that averaging has on the SimCast data. Averaging tends to obscure extreme events, but the general relationship is preserved. Apparently monthly averaging maintains the relationship between predictor and response variables better than daily averaging. Maintenance of relative but not absolute features of model predictions may be a common outcome for other model systems, limiting applications to comparative analyses.

In addition to the importance of metamodels such as the late blight metamodel for ecological analysis and planning, the structure of the resulting metamodels is also of inherent interest.

Ecological models, such as those predicting species distributions or disease risk, transform time series of meteorological data into ecological outcomes, in what can be considered summarizing or aggregating data. It is an empirical question whether use of lower temporal resolution weather data will capture the most important features of a model. De Wit and Van Keulen (1987) suggested that one should 'calculate first, average later'; and Nonhebel (1994) showed that, because of the high variability of the distribution of rainfall in most climates, and the non-linear response of a crop to rainfall, a crop model overestimated potential yield when using monthly rather than daily data. However, these authors did not adjust their models as they aggregated the input data used.

While predictions based on means may not capture all the features resulting from increased variability in the future as a result of climate change (Scherm and van Bruggen 1994), these metamodels are useful tools for decision-making, planning future research and other policy decisions. Rather than being a tool for estimating absolute disease risk, our late blight risk evaluations are a way of efficiently estimating relative rankings of risk over large areas. Because the late blight metamodels maintain relative relationships, despite under predicting blight units, linking these models with a geographic information system supports creation of maps for comparisons between different time-periods under climate change scenarios, or comparisons of different geographic areas during the same time period. These types of information for potato late blight can be useful in planning breeding program locations, making determinations regarding education and extension efforts for areas where disease pressure will increase under future scenarios, or making predictions regarding species invasions.

Metamodels are likely to become more widely used in ecology, particularly in the context of projections of the effect of global climate change (Urban 2005, Piñeros Garcet et al. 2006). Because global circulation models tend to predict larger time periods more accurately than smaller time periods (Sun et al. 2006), it could be desirable to use the larger time-step data in an unmodified format, while being aware of the limitations of this approach. The effects of climate change make

the need to estimate shifts in ecological processes such as disease risk more pressing. Because most available climate change data are not at a temporal resolution that is compatible with many currently used process-based models, modifications such as these are particularly useful. Our comparison of metamodels developed from a process-based ecological model indicates that such an approach can successfully be used to extend the application domain to lower spatial or temporal resolution input data.

Acknowledgments

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