1 **A PREDICTIVE FRAMEWORK TO UNDERSTAND FOREST RESPONSES TO**

2 **GLOBAL CHANGE**

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Predicting forest response to global change

23   ABSTRACT

24   Forests are one of earth's critical biomes. They have been shown to respond strongly to

25   many of the drivers that are predicted to change natural systems over this century,

26   including climate, introduced species, and other anthropogenic influences. Predicting

27   how different tree species might respond to this complex of forces remains a daunting

28   challenge for forest ecologists. Yet shifts in species composition and abundance can

29   radically influence hydrological and atmospheric systems, plant and animal ranges, and

30   human populations, making this challenge an important one to address. Forest ecologists

31   have gathered a great deal of data over the past decades and are now using novel

32   quantitative and computational tools to translate those data into predictions about the fate

33   of forests. Here, after a brief review of the threats to forests over the next century, we

34   describe one of the more promising approaches to making ecological predictions: using

35   hierarchical Bayesian methods to model forest demography and simulating future forests

36   from those models. This approach is able to capture complex processes, such as seed

37   dispersal and mortality, and incorporate uncertainty due to unknown mechanisms, data

38   problems, and parameter uncertainty. After describing the approach, we offer an

39   example by simulating drought for a southeastern forest. We conclude by discussing how

40   this approach and others needs to be cast within a framework of prediction that strives to

41   answer the important questions posed to environmental scientists, but does so with a

42   respect for the challenges inherent in predicting the future of a complex biological

43   system.

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45   **Keywords:** *Bayesian methods, climate, forecasts, forests, global change, models,*

46   *prediction.*

47

47   INTRODUCTION

48   Anticipating forest diversity of the coming century is an important component of global

49   change research. Forests cover more than a third of the earth's land mass. They regulate

50   atmospheric gases, influence hydrological cycles, and provide important ecosystem services to

51   human populations, such as food, fiber, and fuel. Rising atmospheric CO2, climate change,

52   introduced species, and land-cover modification by humans are dramatically altering the

53   distribution, biodiversity, and biogeochemistry of forests. Our understanding of these changes

54   remains rudimentary, despite their relevance for human society. Progress is limited because it

55   has been difficult to assimilate the increasing information now available from field studies and

56   models into a coherent framework for prediction. Here we consider the challenges of

57   assimilation and use a specific example to illustrate how emerging tools can help.

58   The last decade has brought new approaches to modeling and computation, and it is

59   timely to ask how greater exploitation of these advances might help scientists predict future

60   environments. Can increased capacity to assimilate large amounts of information derived from

61   diverse sources help us anticipate landscape change? Although direct calibration of biological

62   responses to the full range of environmental variables is not expected anytime soon, substantial

63   information already exists on how variation in climate, land cover, and CO2 affect individual

64   trees and how these effects can differ across species and communities. Much of this fine-scale

65   information on tree physiology and ecology is hard to merge with the coarse-scale variation in

66   climate, atmospheric CO2, and land cover. The availability of new modeling frameworks and

67   computational tools motivate a fresh look at the prediction problem, with a focus on how fine-

68   scale processes such as the growth and mortality of individual trees are influenced by global

69   change variables and how those responses extrapolate to regional biodiversity.

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70   In this chapter we discuss how prediction is used not so much as a way of forecasting the

71   future, but rather as a means for synthesizing what is known. We briefly review some of the

72   biological processes critical to how forests respond to global change, how these processes affect

73   individuals through demographic rates (growth, survival, and reproduction), and how to place

74   this understanding in a context that permits application of some new modeling and

75   computational tools. We then illustrate a prediction approach with an example from the

76   southeastern United States. We do not advocate this as a means for precise forecasting, but rather

77   as a means for application of current understanding to explore the types of changes that are

78   important for scientific progress and stewardship.

79

80   GLOBAL CHANGE DRIVERS

81 To address how forests might change over the next century ecologists need to focus on processes

82   that are known to be affected by global change and that have been established as important to

83   current forest structure. We review here some of the processes that have been well-studied and

84   might be integrated into predictive models.

85 *Climate change*

86   Climate change is among the most important drivers of forest change, yet ecologists find

87   a   daunting challenge to quantify and anticipate the exact ways in which changing climate will

88   affect forests. Correlations between climate variables and species distributions are only a

89   beginning (Iverson and Prasad 1998). Forest responses to climate change are complicated by

90   biology, because tree populations interact (Canadell et al. 2007, Roe and Baker 2007).

91   Competition, natural enemies, and availability of mutualists influence species distributions, and

92   these influences will change as climate and tree species abundances change.

93   Forest composition will in large part be determined by species' ability to migrate.

94   Changes in geographic distribution of some species are already evident (Parmesan and Yohe

95   2003, McCarty 2001), including northward range shifts and local extinctions at low latitudes and

96   altitudes for small mammal, insect, and bird populations (Thomas et al. 2006, Hitch and Leberg

97   2007, Moritz et al. 2008). Because of the long generation time of trees, one of the few sources of

98   information on potential tree range shifts comes from fossil pollen data. These data show that

99   glacial cycles have caused tree species to undergo repeated range shifts in the past (Williams et

100   al. 2004). However, paleoecological data provide limited insight for contemporary climate

101   change, because change is now more rapid than in the past (Huntley 1991), will result in higher

102   global temperatures than were experienced over the last several million years (Crowley 1990),

103   and is occurring in a different biological setting. Post-glacial migrations occurred in a poorly

104   understood competitive setting, certainly different from that of today. Seeds from potential

105   immigrant species must establish in competition with resident species of intact forests. Under

106   modern conditions, migration capacity of many species will be limited by low fecundity,

107   restricted dispersal, and reduced establishment opportunities (Clark et al. 2001, 2003, McLachlan

108   et al. 2005).

109   Predicting changes in composition within current species ranges is also difficult. An

110   important insight from paleoecology is the apparently idiosyncratic response of many species to

111   past natural warming (Davis 1969, Van Devender 1979, Webb 1986, Prentice et al. 1991, Tinner

112   & Lotter 2001). Novel combinations of climate and edaphic factors, together with dispersal

113   limitation, lead us to expect the emergence of new forest communities supporting reorganized

114   food webs (Saxon et al. 2005, Williams et al. 2007). The rate and magnitude of change will be

115   species-specific, and it will depend on life history (Meunier et al. 2007) as well as on interactions

116   involving mutualists (e.g., pollinators, mychorrizae), competitors, and natural enemies (Ibanez et

117   al. 2006).   Further climate change will interact with disturbance cycles and human land use, as

118   shifts in climate put pressure on how societies use land that is currently covered by forests.

119   *Rising CO$_2$*

120   The direct effects of climate change will be mediated by changes in photosynthetic rates

121   and water use efficiencies under elevated atmospheric CO2 (Long et al. 2004). These processes

122   are observable at leaf scales, but extrapolation to entire forest stands is difficult. Increases in

123   photosynthetic rate and productivity are documented for woody plants, the magnitude of increase

124   depending on resource availability (Curtis and Wang 1998, Ainsworth and Long 2004, Ogren

125   1984). Both models and experiments suggest that species differences may be important for

126   overall response (Bolker et al. 1995, Reich et al. 2001, Mohan et al. 2007). Forest net primary

127   productivity is expected to increase under elevated CO2 (Norby et al. 2005), although free air

128   CO2 experiments (FACE) reveal that tree species' responses differ. For example, loblolly pines

129   (*Pinus taeda*) treated with high CO2 continued to add more wood biomass than control pines

130   over eight years, while sweetgum (*Liquidambar styracaflua*) at another site showed only a

131   transient effect, likely due to differences in allocation of resources derived from CO2 (Moore et

132   al. 2006).

133   Rising CO2 may affect forest composition as well as productivity, shifting community

134   structure through differential effects on maturation and fecundity (LaDeau and Clark 2002) and

135   seedling recruitment (Hattenschwiler and Korner 2000, Sefcik et al. 2007, Mohan et al. 2007).

136   Pines exposed to high CO2 mature at smaller diameters and produce, on average, three times as

137   many cones as control trees (LaDeau and Clark 2001). Any population responding to changes in

138   atmospheric gases to this degree would be expected to increase in abundance at the expense of

139   those that do not.

140   *Introduced and invasive species*

141   Species invasions, especially large-scale outbreaks of exotic pests and pathogens, have

142   occurred with increasing frequency during the past century (Orwig and Foster 1998) and can

143   radically alter forest community structure. Chestnut blight (*Cryphonectria parasitica*), Dutch elm

144   disease (*Ophiostoma spp.*), and gypsy moths (*Lymantria dispar*) are examples of introduced

145   pathogens that have led to severe mortality and near extinction of their host tree species. Current

146   emerging pests and diseases such as sudden oak death (*Phytophthora ramorum*), balsam and

147   hemlock woolly adelgids (*Adelges piceae* and *A. tsugae*), white pine blister rust (*Cronartium*

148   *ribicola*), butternut canker (*Sirococcus clavigignenti-juglandacearum)*, dogwood anthracnose

149   (*Discula* spp.*)*, and beech-bark disease (*Cryptococcus fagisuga)* are causing heavy mortality of

150   their host species (Burdon et al. 2006, Lovett et al. 2006).

151   Invasive plant species often affect native species through competition for resources

152   (Gorchov and Trisel 2003, Martin and Marks 2006), but some also alter soil properties

153   (Heneghan et al. 2006) or exude chemicals toxic to benign competitors or tree mutualists

154   (Stinson et al. 2006). While many invasive species favor disturbed habitats, intact forests may be

155   most vulnerable to invasion by late-successional, shade-tolerant exotics (Martin and Marks

156   2006). The full impact of invasive species, both plant and animal, can be difficult to assess

157   because interactions between exotics and the native community change can lead to 'invasion

158   meltdowns' (Simberloff and Von Holle 1999), where the effects of one invader facilitate others.

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159   *Natural enemies*

160   Along with the critical threat of introduced pathogens, trees may interact with existing

161   native or invading pests and pathogens in new ways under novel climate conditions (Burdon et

162   al. 2006, Harvell et al. 2002, Logan et al. 2003). Some of these changes are already occurring.

163   Recent outbreaks of pests in Europe and North America have been occurring at higher elevations

164   and latitudes than in the past (Logan et al. 2003, Battisti et al. 2005, Woods et al. 2005).

165   Pathogens previously limited by environmental conditions unfavorable to overwintering,

166   reproduction, infection, or other aspects of their life cycles may become more prevalent (Bergot

167   et al. 2006, Harvell et al. 2002, Garrett et al. 2006). Drought and storm damage can increase the

168   impact of insect (Powers et al. 1999) and fungal pathogen outbreaks (Clinton et al. 1993,

169   Desprez-Loustau et al. 2006). Because of their short life-spans and physiological sensitivity to

170   temperature, insects and pathogens may adapt more quickly to new climate regiimes than their

171   host plants (Ayers and Lombardero 2000, Garrett et al. 2006). However, plant defense responses

172   to disease and herbivory will also not remain static (Garrett et al. 2006, Stiling and Cornilissen

173   2007), and the rate at which tree populations can respond to outbreaks will be crucial to

174   determining future patterns of pathogen and pest damage. Although many studies agree that

175   forests generally face increased risks of pest and pathogen damage under climate change,

176   responses will depend on the specific combination of host and pest/pathogen (Cannon 1998, Roy

177   et al. 2004).

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179   HIERARCHICAL MODELING: A PATHWAY TO A PREDICTIVE FRAMEWORK

180   Models cannot capture the full complexity of interactions that result from the direct

181   effects of climate change filtered through biological interactions. Instead, the only hope for

182   learning about the potential responses of forests to climate change must come from models that

183   can account for these potentially complex interactions without explicitly describing them. This

184   is what is meant by 'modeling uncertainty.' Precise specification of the complexity is not

185   feasible, whereas ignoring the uncertainty and complexity will be misleading. Substantial

186   information already exists to aid in model building, but there are also important gaps in our

187   knowledge about forest processes. To exploit what is known, we must therefore develop model

188   depictions of known processes that can be combined with appropriate structures for what is

189   unknown. Hierarchical modeling provides one way of approaching the problem, and serves as a

190   basis for Bayesian prediction. There are many other approaches to predicting forests. Although

191   we focus here on Bayesian demographic modeling, we review other methods in the final section.

192   Anticipating how forests will respond to environmental changes requires models that

193   relate environmental conditions, such as precipitation and temperature, to forest dynamics, such

194   as population change due to mortality and growth. These models must also be able to project

195   those relationships forward under scenarios of future conditions. Further, to make these

196   predictions meaningful, ecologists must allow for the fact that the processes driving forest

197   dynamics are only partially known. There is uncertainty about current conditions used to

198   parameterize the models, unknown aspects of the processes themselves, and uncertainty about

199   future conditions. All can influence predictive distributions for numbers, abundances, and

200   geographical ranges of species. A predictive distribution combines the deterministic relationships

201   that are sufficiently well known to be expressed as functional forms with the uncertainty that

202   comes with observations, specification of the model, and estimation of parameters.

203   Prediction can apply not only to actual future states, but to model and data implications

204   for any time or place where data have not been collected. For example, using a model that was

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205   fitted with light as a covariate (Figure 1), we can construct predictive distributions of a

206   demographic response to light intensities not included in the analysis. The data used for model

207   fitting here include a range of light values, but do not necessarily include the precise values

208   where predictions will be made. The predictive distribution, therefore, needs to integrate over

209   uncertainty in the estimates of the parameters, the observations, and in the model specification,

210   and can thus predict the demographic response over a more continuous range of light values. In

211   this section, we summarize the basic conceptual framework for prediction. We then discuss how

212   simulation models are used in prediction and how different sources of uncertainty enter into this

213   analysis. This section concludes with remarks on how to evaluate the predictions produced by

214   these models.

215   Although there are many important ways to quantify the processes important to forests,

216   from biogeochemical changes to standing biomass, the prediction process we describe here

217   focuses on demographic rates. Changes in demography have a long history in assessments of

218   environmental impacts on population dynamics and health, and can indirectly describe chemical

219   storage and biomass. If we want to understand the past and future of our own species, we turn

220   first to demographic rates. The per-capita population growth rates used to summarize the

221   population dynamics of nations are routinely broken down into birth, death, and migration rates.

222   Epidemiological data are applied to problems of nutrition and disease, with demographic rates

223   being the response variables.

224   Demographic rates of trees provide an important scale for analysis and prediction. Seed

225   bank persistence, seed germination, tree growth, survival, fecundity, and dispersal are the basic

226   demographic rates that can be used to understand the impact of global change on individual trees,

227   and by extrapolation to populations and the forest community. By quantifying how these rates

228   relate to important environmental variables as well as to one another (the number of seeds

229   influences the number of future seedlings, and so on) we can begin to capture the behaviors of

230   forests as dynamic systems, which is essential to substantive prediction. Forest ecologists have

231   long understood the value of modeling at this scale, and a number of important forest simulators

232   use demography as the key dynamic engine for their population forecasts (e.g., FORET, Sortie,

233   ED). We extend this tradition to fully embrace the Bayesian structure for both inference and

234   predictive simulation.

235   *Coupling Bayesian inference and prediction*

236   We focus on the Bayesian framework because it offers a conceptually coherent framework

237   for prediction (Clark 2007a). It is not restricted to a particular model, but rather accommodates

238   many types of data and processes. Traditionally, model forecasts have focused on forward

239   simulation, starting with parameter values and scenarios of change as inputs and producing

240   simulated data as output. Parameterization these models, however, was rarely conducted in a way

241   that properly anticipates the role of uncertainty used for prediction (forward simulation from the

242   model). For example, estimates of model parameters often assume a different model, sometimes

243   even a different scale, from the model used to make predictions (e.g., temperature or CO2

244   dependence at the level of leaves is often used as a basis for simulating canopy response to

245   atmospheric CO2).

246   Extrapolation is easily accomplished under a Bayesian framework where all model

247   parameters are considered random variables. By describing the distributions of those random

248   variables (such as a model for leaf response to CO2), fine-scale relationships can be integrated to

249   produce predictions for larger scales. The result is a set of predictions that are coherent with

250   model fitting—we know where the uncertainty comes from, because there is a quantitative link

251   between data, process, and prediction. The Bayesian approach encourages a view of uncertainty

252   with specific sources, including process, parameter estimates, and observation errors. Process

253   error is especially important because process models are typically crude, representing only a

254   small subset of all known and important interactions. Process error uses stochasticity to account

255   for the variation in processes due to interactions that have not been formally modeled.

256   This hierarchical framework involves specifying the relationships between different parts

257   of the model in the form of conditional probabilities. That is, we understand one component of

258   the model *given* (or 'conditioned on') the status of other components. The data are conditional

259   on an underlying process. Likewise, a process at one scale might be conditioned on a different

260   process at another scale. For example, tree growth depends on light available to the tree. Light

261   availability might, in turn, depend on interception by canopies of other trees. One of the key

262   strengths of the Bayesian framework is the flexibility with which models can be constructed to

263   represent complex problems by combining these relatively simple conditional probabilities. This

264   approach has the flexibility to incorporate numerous sources of data, model output, indirectly

265   observed variables, observation error, and prior information about all parts of the problem that

266   have been gathered from sources such as literature or expert opinion. The key components of

267   such analyses are here termed *process models*, *data models*, and *parameter models* (Clark et al.

268   2003).

269   In our case, process models represent our understanding of how environmental variables

270   influence tree demography. A demographic rate that cannot be measured directly can be

271   represented by a process model informed by relevant data. For example, estimates of fecundity in

272   trees may be informed by seed trap data, a model for how seeds disperse, by observations of

273   flowering, a model of tree maturation, and by data on tree sizes (Clark et al. 2004). Geometric

274   models of canopy light transmission can be related to remote sensing imagery and canopy status

275   observations to estimate the canopy light environment and to hemispherical photography to

276   estimate understory light conditions. Process models can be as simple as a linear relationship or

277   as complex as a system of nonlinear differential equations, such as those used for the atmosphere

278   or hydrological cycles. The process model itself is uncertain, and we would like that uncertainty

279   to be reflected in predictive distributions. Model error is particularly hard to quantify, because

280   the concept of a 'correct' model rarely has clear meaning in environmental science. Processes are

281   influenced by many factors, only a subset of which will be specified.

282   Data models connect observations with an underlying process. Multiple data sets might

283   inform the same process. For example, a process model for tree growth may be informed by

284   both inventory data and tree increment cores, with each dataset having its own data model

285   accounting for the different biases and error distributions (Clark et. al. 2007b).

286   *Parameter models*, the core of model estimation, describe distributions for all model

287   parameters. The posterior distribution of parameters used for inference about parameter

288   significance combines the likelihood distributions with *priors*, distributions based on prior

289   knowledge (or uniform distributions when no prior knowledge is assumed). Further, parameter

290   models can account for hierarchical relationships in the models that may have important

291   influence on inference. For example, we expect the parameters linking growth to light to differ

292   among individuals, which could warrant a random effects prior that quantifies how likely two

293   individuals are to differ in this growth-light relationship. Inference entails estimates of these

294   different contributions to the overall model fit. Prediction combines these estimates with

295   scenarios that involve the model predictors, or 'explanatory variables'.

296   *Using models for predicting future states*

297   Moving from inference to predicting future states adds yet another source of uncertainty

298   to the predictive process—that associated with a hypothesized scenario. If climate variables enter

299   as explanatory variables for tree growth, and we want to predict growth in a different climate

300   setting, we must recognize the uncertainty associated with climate change. If the model is

301   dynamic, then even at the outset of a predictive simulation, the initial conditions are uncertain.

302   Initial conditions may be set to observations (see below), but many variables may be unobserved.

303   Boundary conditions are often based on scenarios about the future state of the system. Scenarios

304   may include the best estimates of experts or the output of other models, having uncertainties of

305   their own. Bayesian analysis allows for uncertainty in initial states and boundary conditions.

306   Ideally, predictive distributions integrate uncertainty from all of these sources.

307

BOX 1: A taxonomy of uncertainty could include sources of error summarized here:

- Process error – Uncertainty in the process model. Variation affects dynamics and can compound over time.

- Measurement error – Discrepancy between observations and true process state. Measurement error can, but does not have to be propagated to predictions.

- Random individual and temporal effects (RITES) – individual effects refer to uncertainty that is associated with individuals (such as differences created by genetic variation) and over time. Temporal uncertainty can apply to all individuals at once, but changes over time (e.g., seed masting in trees).

- Initial condition uncertainty – Error in the specification of the initial state of a predictive simulation

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> - Scenario uncertainty – Uncertainty in the variables that describe predicted scenarios (e.g., temperature means over the next one hundred years).

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309   It is important to interpret predictive distributions appropriately. Some ecological

310 processes are highly predictable, for reasons that are well understood. Leaf area index can often

311 be predicted based on local hydrology (Grier and Running 1977). Other processes, such as long

312 distance dispersal, are inherently unpredictable despite confident parameter estimates for

313 dispersal kernels (Clark et al. 2003). Still other processes depend on uncertain scenarios, such as

314 CO_2 acclimation.

315   Because many climate-change phenomena are complex, with many potential sources of

316 error, predictive distributions may often be less useful for anticipating the future than they are for

317 analyzing how different sources of uncertainty contribute to our understanding of a process. This

318 understanding can then be used to prioritize research needs and direct future field research and

319 experiments designed to reduce forecast uncertainty.

320 *The inference stage*

321   Predicting forest change requires a series of steps that link observations on individual trees

322 to computer simulations of entire forest stands under anticipated climate scenarios. To illustrate

323 these concepts we discuss an application where hierarchical models were fitted to data including

324 estimation of measurement error, process error, and parameter error, all of which are propagated

325 to predictive distributions based on scenarios for soil moisture.

326   Prediction begins with inference, the estimation of parameter values for the model.

327 **Error! Reference source not found.** shows how different sources of uncertainty contribute to a

328 predictive interval around the relationship between the diameter of a tree and its growth rate. In

329 this figure growth rates of adult trees are predicted for a range of diameters at two light levels for

330 *Quercus rubra*. For this example of diameter growth, the size of the predictive intervals

331 illustrates how year-to-year variation dominates over individual differences, parameter

332 uncertainty and model uncertainty. In other words, annual variation is large and not well

333 described based on the covariates in the model, which include light availability, tree diameter,

334 and growth the previous year. However, individual differences and parameter uncertainty are

335 relatively small. This combination of process and uncertainty will be further discussed in an

336 example that follows.

337   An analysis of uncertainty can help us understand population dynamics even when

338 processes are poorly specified. Figure 3 shows how predictive intervals can be used to assess

339 goodness of fit. The predictive distributions shown in **Error! Reference source not found.** can

340 be used to simulate growth rates of trees, averaging over all sources of variation (dashed lines in

341 Figure 3). For comparison, the green lines in Figure 3 show growth trajectories of actual trees

342 based on tree rings measured from increment core samples. The bounds of the predicted growth

343 trajectories are not based on models of how age relates to diameter increment. Instead these

344 trajectories were estimated purely from the process model of growth over time, given

345 uncertainty. Every year growth is estimated from covariates and the diameter change is

346 calculated.

347   To incorporate species interactions in the model, we use a simulator where trees intercept

348 light, thereby shading their neighbors. Scenarios involving soil moisture fluctuation allow us to

349 explore the consequences of climate change in the context of competition among trees for light.

350 We use the Scalable Landscape, Inference and Prediction (SLIP) simulator (Govindarajan et al.

351 2007) which combines the demographic rate models to project individuals forward. SLIP differs

352 from other forest simulators (e.g., SORTIE, JABOWA, FORET) in that it incorporates

353 uncertainty estimated at each stage of the model described above. In the SLIP predictions,

354 interacting individuals grow, survive, and reproduce using the same model fitted to data over a

355 landscape grid of 512 by 512 meters. We incorporate not only responses to covariates but also

356 the estimated variation across years and among individuals (RITES, see box 1) and uncertainty

357 in the processes model. Trees compete for light, and the largest trees create the light

358 environment experienced by smaller trees.

359   To complete the path from data to prediction under changing climate, we can compare

360 model runs with current climate variables (temperature and soil moisture) with those run under

361 scenarios that reflect anticipated shifts in southeastern climate patterns. This final section

362 describes how SLIP simulated forest dynamics under a scenario of periodic extreme drought.

363 *A drought example*

364   Droughts are predicted to occur in the southeastern US with greater frequency and

365 intensity in the coming century (Mearns et al. 2003).   The structure of forests in the Southeast

366 may depend on whether or not and which deep-rooted forest trees are buffered from increasingly

367 arid climate. If adults remain connected to a deep water supply, while shallow-rooted seedlings

368 fail to survive, we could experience a gradual shift to Mediterranean-like conditions.

369   For a simple demonstration, we vary soil moisture stochastically, with an underlying

370 periodic signal (a simple sine function with random noise). As a control, we assumed a mean

371 and variance for the observed soil moisture data that are uncorrelated across years. In these

372 simulations we include soil moisture effects only at the stages of germination and seedling

373   growth and mortality. These simulations address the extent to which large trees might be

374   buffered against increased aridity, whereas shallow-rooted seedlings are not.

375   **Error! Reference source not found.** shows modeled relationships between the seedlings

376   of three different species (corresponding to the three columns), *Acer rubrum*, *Liriodendron*

377   *tulipifera*, and *Quercus rubra* and light and soil moisture. These relationships were estimated

378   from data in field experiments (Ibanez et al. 2007) using a logistic regression. The *z*-axis marks

379   predicted annual seedling growth in centimeters of height, and the *x*- and *y*-axes mark percent of

380   total solar radiation reaching the understory and percent moisture content in the soil respectively.

381   The first row of **Error! Reference source not found.** shows the process model (the

382   deterministic model without uncertainty). Light has a strong positive effect on growth, while soil

383   moisture has a more subtle effect. These relationships differ for different species. In rows 2,

384   every point on the graph was changed by adding a random variable drawn from the distribution

385   of process error, so that for every combination of light and soil moisture, possible changes in

386   expected height due to process error are illustrated. Under poor conditions, even with positive

387   values for process error, there is no growth (the flat plateaus under low light or low soil moisture

388   values). Note too that different species have different levels of process uncertainty. *Q. rubra*

389   shows greater differences from the deterministic process we modeled. That is, for *Q. rubra* light

390   and soil moisture fail to capture many of the determinants of seedling growth, where for *L.*

391   *tulipifera*, soil moisture and light explain a good deal of seedling growth. In the third row

392   random draws from both process error and individual effects have been added to the

393   deterministic value of growth predicted with the environmental variables. This illustrates

394   potential deviations from the deterministic kernel due to unmodeled processes.

395   Given the large number of seedlings and the highly dynamic understory light

396   environment of intact forests, inferring large-scale population dynamics under periodic droughts

397   from the estimated growth of seedlings alone would be unrealistic. Seedlings grow to become

398   adult trees, which shade seedlings, and individuals attain adulthood (or not) due to many

399   processes, all of which differ between species. To understand how the entire forest system will

400   respond to drought, therefore, we need to integrate these effects over the behavior of all forest

401   trees, not just seedlings.

402   We ran five replicates of the control and the drought treatment over 200 simulated years,

403   with a starting forest based on the observed abundances and sizes of 30 tree species from the

404   Duke Forest in central North Carolina. We found a clear response to drought in the forest, but

405   also resilience in key community-level patterns (Figure 5**Error! Reference source not found.**).

406   Seedling densities (Figure 5a), as predicted by our inference based on process models, oscillated

407   with soil moisture levels. Although the roughly 50% drop in seedling densities did translate into

408   fewer saplings (which includes stems between 0.5m and 2m tall) (Figure 5b), the duration of the

409   drop in sapling number and the speed of recovery at the end of drought showed a diminished

410   response as compared to that of seedling densities. This modeled tolerance of periodic drought is

411   even more pronounced as the size class of trees increases. Adult densities and growth showed

412   little response to drought cycles (**Error! Reference source not found.**c). Although stem

413   numbers did fluctuate, they did so very close to the range of the control runs. Thus, adult stems

414   were not reduced to savannah-like densities even though seedling mortality during droughts was

415   high.

416   In order to draw inference for this experiment, we return to how uncertainty entered the

417   model and the simulations. In this example, we ran five replicates of the two treatments. These

418   repeated runs, although not extensive, show how sensitive our inference is to the model's

419   stochastic components. Process error and RITES were included in these runs, so that at the scale

420   of individuals and years, uncertainty entered in every vital rate, and did so differently for

421   different species. Despite these sources of uncertainty, the abundances and densities of tree life

422   history stages were remarkably consistent over the runs.

423   To generate more informed predictive distributions, we would need to run the simulations

424   more times, but the trend is obvious in this example. The patterns we see in densities over time

425   also seem robust to the high degree of stochasticity modeled here—drought treatments behave

426   similarly and control runs behave similarly across replicates. Importantly, however, we included

427   no uncertainty in our initial conditions or predictive scenarios. We assumed a specific starting

428   forest composition and constructed a soil moisture regime as input that implied no uncertainty in

429   either soil moisture over the next 200 years or in the forests initial composition. We know that

430   changes in sequence, frequency, and intensity of the drought scenarios modeled would strongly

431   influence how the forest behaves (which will be discussed in more detail in the concluding

432   section).

433   A single experiment does not have to accommodate every potential source of uncertainty.

434   Any inference drawn from model results, however, must be restricted by how uncertainty enters

435   the model. The above drought simulation tests a hypothesis focused on a specific mechanism:

436   could adult trees that are not affected by rare drought events buffer the overall forest from

437   droughts that damage seedlings and saplings? We can deduce from these experiments that more

438   frequent drought or longer drought periods might eventually influence adult population and

439   forest biomass. The important inference for this simulation is that the forest as a whole may be

440   buffered from extreme drought events that only affect early life-history stages. Results such as

441   this one do not contribute much to an overall prediction of forest change, but can contribute to a

442   toolbox of information essential for developing forecasts. The final section discusses how

443   forecasting can combine data, models of ecological processes, and climate scenarios to create a

444   protocol for prediction.

445

446   A NEW FORECASTING PROTOCOL BASED ON PROCESS

447   The root of model-based prediction lies in model-based inference. The goal of the

448   inference stage of analysis is to fit a deterministic core of a model (e.g., "how trees respond to

449   the environment") and to partition unexplained variance in a way that can help the model realize

450   the variety of possible futures based on how little we know now. The importance of the

451   deterministic portion of a model for prediction is well understood by ecologists (it's our job), but

452   the impacts of the error and how it is partitioned are less appreciated. Most ecological models

453   intended for forecasting drop the residual error entirely, or treat the error as additive Gaussian

454   white noise. There is a growing recognition of the need to include autocorrelation in space and

455   time, but modern statistical methods also allow for the inclusion of non-additive effects, such as

456   the variation of model parameters in space and time as well as hierarchical random effects at all

457   levels, down to every tree having its own parameters as shown in the example above. Also as

458   demonstrated in our example, data models allow the separation of various forms of measurement

459   error from process error, which is critical in ecology as variability is often dominated by true

460   differences among individuals, sites, or samples rather than measurement error. The treatment of

461   variability may not only affect the predictive variance, but also the mean and even our

462   understanding of the dynamics of the process, such as the mechanisms for species coexistence

463   (Clark et al. 2007a).

464   Moving from inference to prediction introduces a number of additional sources of

465   uncertainty. Forward simulation requires the specification of both *initial conditions*, which

466   describe the initial state of the model, and *boundary conditions*, which describe the time-

467   evolution of model constraints. The specification of initial conditions is often based on data, but

468   the initial values of all state variables are rarely observed completely, and there are often

469   multiple datasets that can inform the initial state. Determining the initial conditions can

470   therefore be a challenging problem of statistical inference at the start. Although this type of

471   statistical modeling is not currently common in the ecological literature, it is a backbone of

472   inference in meteorology where it is referred to as *data assimilation*. The classical tools for this

473   inference in data assimilation have been variants of the Kalman filter (Kalman 1960), which

474   estimates the dynamics of a system based on sparse measurements of its characteristics. Newer

475   hierarchical Bayes approaches are both more flexible and less complicated (Wikle and Berliner

476   2007). Boundary conditions, on the other hand, are often developed based on scenarios about the

477   future state of the system, and thus all forecasts are made conditional on these scenarios.

478   Scenarios may include the best estimates of experts, maximum and minimum range bounding

479   scenarios, or the output of other models with their own uncertainty. For example, the IPCC uses

480   expert opinion and socioeconomic models to develop a standard set of climate change scenarios

481   that are boundary conditions for gas emissions, land use change, and development within GCMs

482   (IPCC 2000, IPCC 2007). The outputs of GCMs routinely become the input scenarios for forest

483   biogeochemistry and biodiversity models (e.g. VEMAP). Obviously scenarios and the forecasts

484   made from them cannot be expected to be true, since the information provided by forecasts can

485   alter the behavior of the agents involved, but they are useful precisely because they provide us

486   with information that allows us to alter our behavior.

487   Another critical component of forecast uncertainty comes from model choice. Model

488   choice error is particularly hard to quantify, since all probability statements are conditional on

489   the model implemented or upon a finite set of alternate models, rather than the infinite set of all

490   possible models. Information theory and model selection can help us choose between alternate

491   model forms, or to weight models for model averaging (Burnham and Anderson 2002); however,

492   such statistical measures are not a substitute for an experts understanding of the system nor do

493   they guard against errors in our conceptual understanding of the system. It is often a useful

494   exercise to compare forecasts generated by different models produced by different research

495   teams; however, such models are never truly independent samples since they often encapsulate

496   the same understanding and even share sub-models as a whole (e.g. almost all ecosystem models

497   estimate photosynthesis using the Farquhar et al. (1980) model).

498   Finally, a critical component of forecasting is to understand the predictability of the

499   process and the factors limiting better prediction. Some ecological processes are very

500   predictable. For example leaf area index tends to vary little for closed-canopy forests around the

501   world. Other processes, such as long distance dispersal, are inherently unpredictable: once the

502   parameters involved are reasonably constrained, collecting reams of additional data will not

503   drastically improve prediction. Ecological processes also vary widely in the temporal horizon

504   for accurate prediction. Some processes are clearly sensitive to initial conditions, while others,

505   such as forest succession, tend to have strong feedbacks that cause dynamics to converge over

506   time. Processes also differ in the extent to which we can consider their parameters fixed versus

507   varying in time and space, especially in the face of novel environmental change. The analysis of

508   models with the proper propagation of error will itself be a critical component of understanding

509   the main sources of uncertainty. This understanding can then be used to prioritize research needs

510   and direct future field research and experiments designed to reduce forecast uncertainty.

511   It is easy to become overwhelmed by the urgency and complexity of current changes in

512   ecological systems. By working together with climate scientists, forest ecologists and managers,

513   statisticians and computer scientists, and paying careful attention to details of ecological systems

514   and how they extrapolate to produce patterns in communities and regions, we can develop

515   forecasts, learn from them, improve them, and re-develop them in the hope that along the way,

516   our informed answers will have a positive impact on how our society responds to these changes.

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521   REFERENCES

522 Ainsworth, E.A.; Long, S.P. 2005. What have we learned from 15 years of free-air CO2
523   enrichment (FACE)? A meta-analytic review of the responses of photosynthesis, canopy.
524   New Phytologist 165 (2): 351-371.

525 Battisti, A., M. Stastny, S. Netherer, C. Robinet, A. Schopf, A. Roques, and S. Larsson. 2005.
526   Expansion of geographic range in the pine processionary moth caused by increased
527   winter temperatures. Ecological Applications 15:2084-2096.

528 Bergot, M., E. Cloppet, V. Perarnaud, M. Deque, B. Marcais, and M. L. Desprez-Loustau. 2004.
529   Simulation of potential range expansion of oak disease caused by *Phytophthora*
530   *cinnamomi* under climate change. Global Change Biology 10:1539-1552..

531 Bolker, B.M., S.W. Pacala, F.A. Bazazz, C.D. Canham, and S.A. Levin 1995. Species diversity
532   and ecosystem response to carbon dioxide fertilization: conclusions from a temperate
533   forest model. Global Change Biology 1(5): 373-381.

534 Burdon, J.J.; Thrall, P.H.; Ericson, L. 2006. The current and future dynamics of disease in plant
535   communities. Annual Review Of Phytopathology 44: 19-39.

536 Buizza, R. and T.N. Palmer. 1995. The singular-vector structure of the atmospheric global
537   circulation. Journal of the Atmospheric Sciences: 52(9): 1434-1456

538 Burnham K.P. and D.R. Anderson. 2002. Model selection and multimodel inference: a practical
539   information-theoretic approach. New York. Springer.

     Canadell, J. G., M. U. F. Kirschbaum, W. A. Kurz, M. J. Sanz, B. Schlamadinger, and Y.
           Yamagata. 2007. Factoring out natural and indirect human effects on terrestrial carbon
           sources and sinks. Environmental Science & Policy **10**:370-384.

540 Cannon, R.J.C. 1998. The implications of predicted climate change for insect pests in the UK,
541   with emphasis on non-indigenous species. Global Change Biology 4 (7): 785-796.

542 Clark, J. S., J. Mohan, M. Dietze, and I. Ibanez. 2003. Coexistence: how to identify trophic
543   tradeoffs. Ecology, 84:17-31

     Clark, J. S., S. R. Carpenter, M. Barber, S. Collins, A. Dobson, J. A. Foley, D. M. Lodge, M.
           Pascual, R. Pielke, W. Pizer, C. Pringle, W. V. Reid, K. A. Rose, O. Sala, W. H.
           Schlesinger, D. H. Wall, and D. Wear. 2001. Ecological forecasts: An emerging
           imperative. Science **293**:657-660.

544 Clark, J. S., M. Dietze, P. Agarwal, S. Chakraborty, I. Ibanez, S. LaDeau, and M. Wolosin.
545   2007a. Resolving the biodiversity debate. Ecology Letters, 10: 647–662

546 Clark, J. S., M. Wolosin, M. Dietze, I. Ibanez, S. LaDeau, M. Welsh, B. Kloeppel. 2007b. Tree
547   growth inference and prediction from diameter censuses and ring widths. Ecological
548   Applications **17**(7): 1942-1953.

549 Clark, J.S., S. LaDeau, and I. Ibanez. 2004. Fecundity of trees and the colonization-competition
550   hypothesis, Ecological Monographs, 74:415-442

551 Crowley, T. J. 1990 Are there any satisfactory geologic analogs for a future greenhouse
552   warming? Journal of Climate, 3: 1282–1292.

553 Curtis, P. S.; Wang, X. Z. 1998. A meta-analysis of elevated CO2 effects on woody plant mass,
554   form, and physiology. Oecologia 113 (3): 299-313.

555 Davis, M. B. 1969. Climatic changes in southern connecticut recorded by pollen deposition at
556   Rogers lake. Ecology 50:409-422.

557 Farquhar G.D., von Caemmerer S., Berry J.A. 1980. A biochemical model of photosynthetic
558   CO2 assimilation in leaves of C3 species. Planta 149: 78-90

559 Garrett, K. A., S. P. Dendy, E. E. Frank, M. N. Rouse, and S. E. Travers. 2006. Climate change
560   effects on plant disease: Genomes to ecosystems. Annual Review of Phytopathology
561   44:489-509.

Govindarajan, S., M. C. Dietze, P. K. Agarwal, and J. S. Clark. 2007. A scalable algorithm for
      dispersing population. Journal of Intelligent Information Systems **29**:39-61.

562 Gorchov, D. L., and D. E. Trisel. 2003. Competitive effects of the invasive shrub, *Lonicera*
563   *maackii* (Rupr.) Herder (Caprifoliaceae), on the growth and survival of native tree
564   seedlings. Plant Ecology 166:13-24.

565 Gramacy, R.B., H.K.H. Lee, W.G. Macready. 2004. Parameter Space Exploration With
566   Gaussian Process Trees. Proceedings of the International Conference on Machine
567   Learning, pp. 353-360.

568 Grier, C. G. and S. W. Running. 1977. Leaf Area of Mature Northwestern Coniferous Forests:
569   Relation to Site Water Balance. Ecology.

570 Harvell, CD; Mitchell, CE; Ward, JR; Altizer, S; Dobson, AP; Ostfeld, RS; Samuel, MD. 2002.
571   Ecology - Climate warming and disease risks for terrestrial and marine biota. Science 296
572   (5576): 2158-2162.

573 Hattenschwiler, S; Korner, C. 2000. Tree seedling responses to in situ CO2-enrichment differ
574   among species and depend on understorey light availability. Global Change Biology 6
575   (2): 213-226.

576 Heneghan, L., F. Fatemi, L. Umek, K. Grady, K. Fagen, and M. Workman. 2006. The invasive
577   shrub European buckthorn (Rhamnus cathartica, L.) alters soil properties in Midwestern
578   US woodlands. Applied soil ecology 32:142-148.

579 Huntley, B. 1991. How Plants Respond to Climate Change: Migration Rates, Individualism and
580   the Consequences for Plant Communities Annals of Botany 67: 15-22.

581 Ibanez, I., J. S. Clark, M. Dietze, K. Feeley, M. Hersh, S. LaDeau, A. McBride, N. E. Welch, and
582   M. S. Wolosin. 2006. Predicting biodiversity change: outside the climate envelope,
583   beyond the species-area curve. Ecology 87:1896-1906.

Ibanez, I., J. S. Clark, S. LaDeau, and J. H. R. Lambers. 2007. Exploiting temporal variability to
      understand tree recruitment response to climate change. Ecological Monographs **77**:163-
      177.

584 Intergovernmental Panel on Climate Change. 2000. Special Report on Emissions Scenarios: A
585   Special Report of Working Group III of the Intergovernmental Panel on Climate Change.
586   N. Nakicenovic and R. Swark (eds.) Cambidge University Press

587 Intergovernmental Panel on Climate Change. 2007. Climate change 2007: the physical science
588   basis. Cambridge University Press, Cambridge, UK.

589 Iverson, L. R., and A. Prasad. 1998. Predicting abundance of 80 tree species following climate
590   change in the Eastern United States. Ecological Monographs 68:465-485.

591 Kennedy, M. and O'Hagan, A. (2001). Bayesian calibration of computer models (with
592   discussion). Journal of the Royal Statistical Society, Series B. 63, 425-464.

593 Kennedy, M. C., Anderson, C. W., Conti, S. and O'Hagan, A. (2006). Case studies in Gaussian
594   process modelling of computer codes. Reliability Engineering and System Safety, 91,
595   1301-1309.

596 Kennedy, M. C., O'Hagan, A., Anderson, C. W., Lomas, M., Woodward, F. I., Heinemeyer, A.
597   and Gosling, J. P. 2007. Quantifying uncertainty in the biospheric carbon flux for
598   England and Wales. Research Report No. 564/06, Department of Probability and
599   Statistics, University of Sheffield. To appear in Journal of the Royal Statistical Society,
600   Series A.

601 LaDeau, S., and J. S. Clark. 2001. Rising CO2 levels and the fecundity of forest trees. Science
602   292:95-98.

603 Logan, J. A., J. Regniere, and J. A. Powell. 2003. Assessing the impacts of global warming on
604   forest pest dynamics. Frontiers in Ecology and the Environment 1:130-137

605 Long, SP; Ainsworth, EA; Rogers, A; Ort, DR. 2004. Rising atmospheric carbon dioxide: Plants
606   face the future. Annual Review Of Plant Biology 55: 591-628.

607 Lovett, G. M., C. D. Canham, M. A. Arthur, K. C. Weathers, and R. D. Fitzhugh. 2006. Forest
608   ecosystem responses to exotic pests and pathogens in eastern North America. Bioscience
609   56:395-405.

610 Martin, P. H., and P. L. Marks. 2006. Intact forests provide only weak resistance to a shade-
611   tolerant invasive Norway maple (*Acer platanoides* L.). Journal of Ecology 94:1070-1079.

612 McCarty, J.P. 2001. Ecological consequences of recent climate change. Conservation Biology
613   15:320-331.

614 McLachlan, J. S., J. S. Clark, and P. S. Manos. 2005. Molecular indicators of tree migration
615   capacity under rapid climate change. Ecology 86:2088-2098.

616 Mearns, L. O., F. Giorgi, L. McDaniel, and C. Shields. 2003. Climate scenarios for the
617   southeastern U.S. based on GCM and Regional model simulations. Climatic Change
618   60:7–35.

     Meunier, C., L. Sirois, and Y. Begin. 2007. Climate and *Picea mariana* seed maturation
         relationships: a multi-scale perspective. Ecological Monographs **77**:361-376.

619 Mohan, JE; Clark, JS; Schlesinger, WH. 2007. Long-term CO2 enrichment of a forest
620   ecosystem: Implications for forest regeneration and succession. Ecological Applications
621   17 (4): 1198-1212.

622 Moore, D. J. P., S. Aref, R. M. Ho, J. S. Pippen, J. G. Hamilton, and E. H. De Lucia. 2006.
623   Annual basal area increment and growth duration of *Pinus taeda* in response to eight
624   years of free-air carbon dioxide enrichment. Global Change Biology 12:1367-1377.

625 Moritz, C. et al. 2008. Impact of a century of climate change on small-mammal communities in
626   Yosemite National Park, USA. Science 322:261-264.

627 Norby, RJ; DeLucia, EH; Gielen, B; Calfapietra, C; Giardina, CP; King, JS; Ledford, J;
628   McCarthy, HR; Moore, DJP; Ceulemans, R; De Angelis, P; Finzi, AC; Karnosky, DF;
629   Kubiske, ME; Lukac, M; Pregitzer, KS; Scarascia-Mugnozza, GE; Schlesinger, WH;
630   Oren, R. 2005. Forest response to elevated CO2 is conserved across a broad range of
631   productivity. Proceedings of the National Academy of Sciences. 102 (50): 18052-18056.

632 O'Hagan, A. 2006. Bayesian analysis of computer code outputs: a tutorial. Reliability
633   Engineering and System Safety, 91, 1290-1300

634 Oakley, J. and O'Hagan, A. 2002. Bayesian inference for the uncertainty distribution of computer
635   model outputs. Biometrika 89, 769-784.

636 Ogren, W.L. 1984. Photorespiration: Pathways, regulation, and modification. Annual Review of
637   Plant Physiology. 35:415-452.

638 Orwig, D. A., and D. R. Foster. 1998. Forest response to the introduced hemlock woolly adelgid
639   in southern New England, USA. Journal of the Torrey Botanical Society 125:60-73.

640 Parmesan, C., and G. Yohe. 2003. A globally coherent fingerprint of climate change impacts
641   across natural systems. Nature 421:37-42.

642 Prentice, I.C., P.J. Bartlein, and T. Webb III. 1991. Vegetation and Climate Change in Eastern
643   North America Since the Last Glacial Maximum. Ecology 72: 2038-2056.

644 Raftery, A.E., T. Gneiting, F. Balabdaoui, M. Polakowski. 2005. Using Bayesian Model
645   Averaging to calibrate forecast ensembles. Monthly Weather Review 133: 1155-1174.

     Rebele, F. 1992. Colonization and Early Succession On Anthropogenic Soils. Journal of
         Vegetation Science **3**:201-208.

646 Reich, P.B., J. Knops, D. Tilman, J. Craine, D.S. Ellsworth, M. Tjoelker, T. Lee, D. Wedin, S.
647   Naeem, D. Bahauddin, G. Hendry, S. Jose, K. Wrage, J. Goth, and W. Bengston 2001.
648   Plant diversity enhances ecosystem responses to elevated CO2 and nitrogen deposition.
649   Nature 410:809-812.

     Roe, G. H. and M. B. Baker. 2007. Why is climate sensitivity so unpredictable? Science
         318:629-632.

650 Roy, B. A., S. Gusewell, and J. Harte. 2004. Response of plant pathogens and herbivores to a
651   warming experiment. Ecology 85:2570-2581.

652 Sacks, J., Welch, W., Mitchell, T.J., and Wynn, H.P. 1989. Design and Analysis of Computer
653   Experiments. Stat. Sci. 4: 409-435.

654 Saxon, E., B. Baker, W. Hargrove, F. Hoffman, and C. Zganjar. 2005. Mapping environments at
655   risk under different global climate change scenarios. Ecology Letters 8:53-60.

656 Sefcik, LT; Zak, DR; Ellsworth, DS. 2007. Seedling survival in a northern temperate forest
657   understory is increased by elevated atmospheric carbon dioxide and atmospheric nitrogen
658   deposition. Global Change Biology 13 (1): 132-146.

Simberloff, D. and B. Von Holle. 1999. Positive interactions of nonindigenous species:
    invasional meltdown? Biological Invasions **1**:21-32.

659 Stiling, P; Cornelissen, T. 2007. How does elevated carbon dioxide (CO2) affect plant-herbivore
660   interactions? A field experiment and meta-analysis of CO2-mediated changes on plant
661   chemistry and herbivore performance. Global Change Biology 13 (9): 1823-1842.

662 Stinson, K. A., S. A. Campbell, J. R. Powell, B. E. Wolfe, R. M. Callaway, G. C. Thelen, S. G.
663   Hallett, D. Prati, and J. N. Klironomos. 2006. Invasive plant suppresses the growth of
664   native tree seedlings by disrupting belowground mutualisms. PLoS Biology 4:e140.

665 Thomas, C. D., A. M. A. Franco, and J. K. Hill. 2006. Range retractions and extinction in the
666   face of climate warming. TREE 21.

667 Tinner, W., and A.F. Lotter. 2001. Central European vegetation response to abrupt climate
668   change at 8.2 ka. Geology 29(6):551-554.

669 Van Devender, T. R. and W. G. Spaulding. 1979. Development of Vegetation and Climate in the
670   Southwestern United States. Science.

671 Webb, T.III. 1986. Is vegetation in equilibrium with climate? How to interpret late-Quaternary
672   pollen data. Plant Ecology. 67(2): 75-91.

673 Wikle, C.K., and L.M. Berliner. 2006. A Bayesian tutorial for data assimilation. Physica D. in
674   press.

675 Williams, A.L., K.E. Wills, J.K. Janes, J.K. Vander Schoor, P.C.D. Newton, and M.J. Hovenden
676   2007. Warming and free-air CO2 enrichment alter demographics in four co-occurring
677   grassland species. New Phytologist. 176:365-374.

678 Williams, J.W.,B.N. Schuman, T. Webb,P.J. Bartlein,P.L. Leduc. 2004. Late-Quaternary
679   vegetation dynamics in North America: scaling from taxa to biomes. Ecological
680   Monographs 74(2):309-334.

681 Williams, J. W., S. T. Jackson, and J. E. Kutzbach. 2007. Projected distributions of novel and
682   disappearing climates by 2100 AD. PNAS 104:5738-5742.

683 Woods, A., K. D. Coates, and A. Hamann. 2005. Is an unprecedented *dothistroma* needle blight
684   epidemic related to climate change? Bioscience 55:761-769.

685

Predicting forest response to global change

685   *Figure captions*

686   Figure 1. Predicted seed production across a light gradient for Acer rubrum. Light is measured

687   as the log of canopy area exposed to direct sunlight estimated from aerial photographs and

688   ground observations.

689   Figure 2. Posterior mean estimates of latent states (green dots) and predictive intervals for low

690   (black) and high (red) canopy exposure (λ is an estimate of the canopy area exposed to full

691   sunlight). Black predictive intervals for low light, from narrow to wide, are parameter

692   uncertainty (dashed), random individual effects (dotted), year-to-year variation (dashed), and

693   process error (not visible). For high light (red) only predictive mean and year-to-year variation

694   are shown.

695   Figure 3. Comparison of increment data from tree rings (green) and predictive distributions of

696   tree diameter.

697   Figure 4. Example simulations of the response of seedling growth to soil moisture and light for

698   three species: A. rubrum, L. tulipifera, and Q. rubra. The three rows show a) the deterministic

699   relationship between covariates and growth, b) an instance where process error has been drawn

700   for each individual from the process error distribution estimated from data, and c) where

701   instances of individual effects as well as process error are drawn from their respective

702   distributions. Error is represented by drawing random deviations from the error distributions,

703   and therefore are examples of the uncertainty and not the actual estimated error terms in order to

704   visualize the variance due to error.

705   Figure 5. Time series for five separate 200 year simulation runs with drought treatments (red

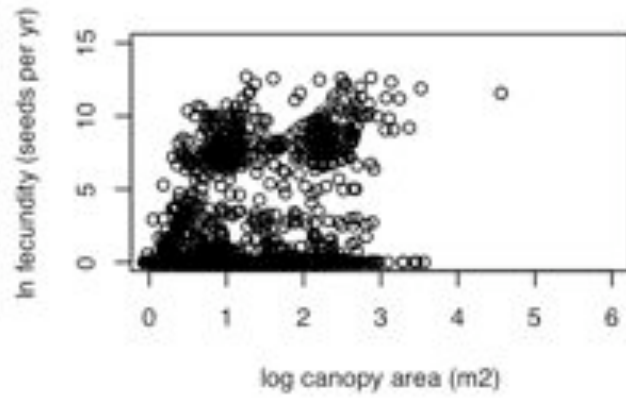706   lines) and without (black lines). Note log y-axes for saplings.

707

Figure 1. Predicted seed production across a light gradient for *Acer rubrum*. Light is
measured as the log of canopy area exposed to direct sunlight estimated from aerial
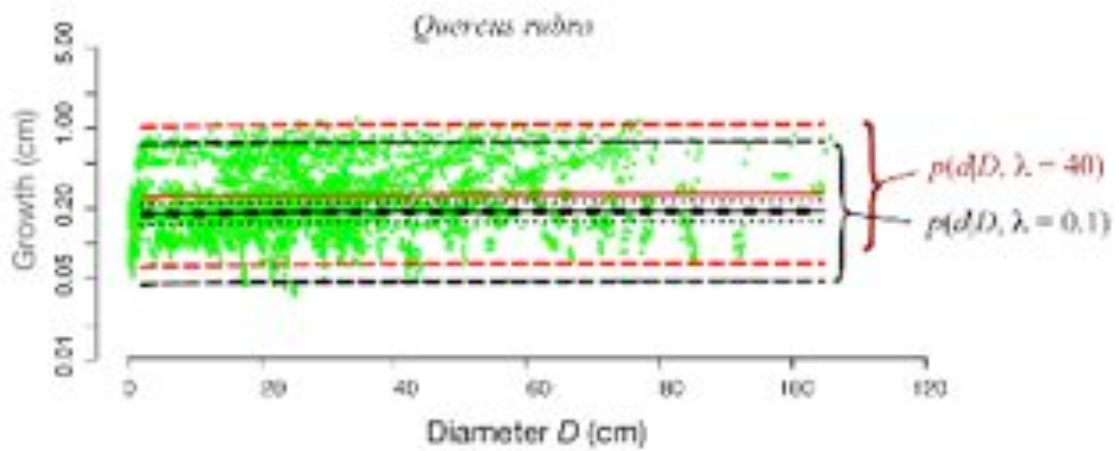photographs and ground observations.

Figure 2. Posterior mean estimates of latent states (green dots) and predictive intervals for low (black) and high (red) canopy exposure (λ is an estimate of the canopy area exposed to full sunlight). Black predictive intervals for low light, from narrow to wide, are parameter uncertainty (dashed), random individual effects (dotted), year-to-year variation (dashed), and process error (not visible). For high light (red) only predictive mean and year-to-year variation are shown.
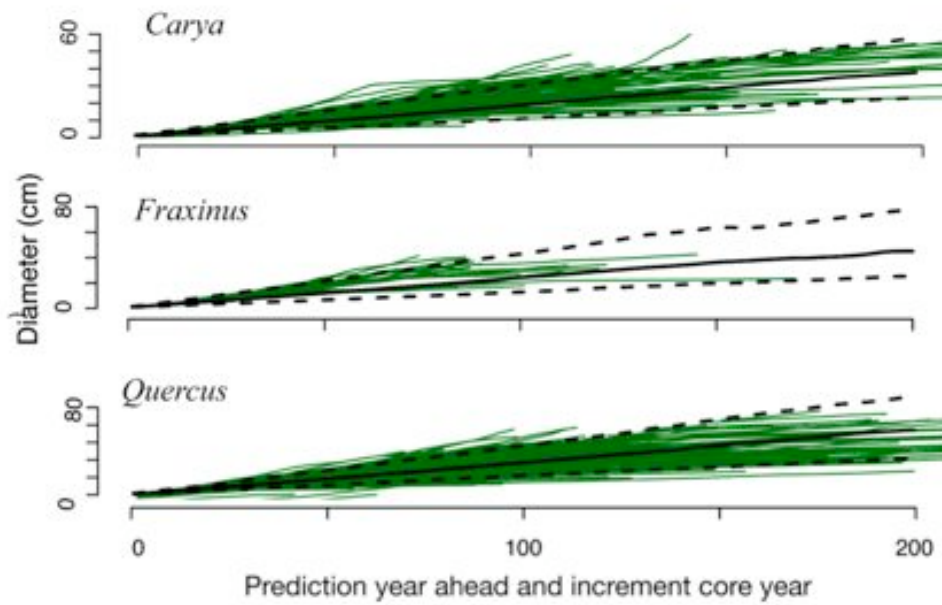
Figure 3. Comparison of increment data from tree rings (green) and predictive distributions of tree diameter.
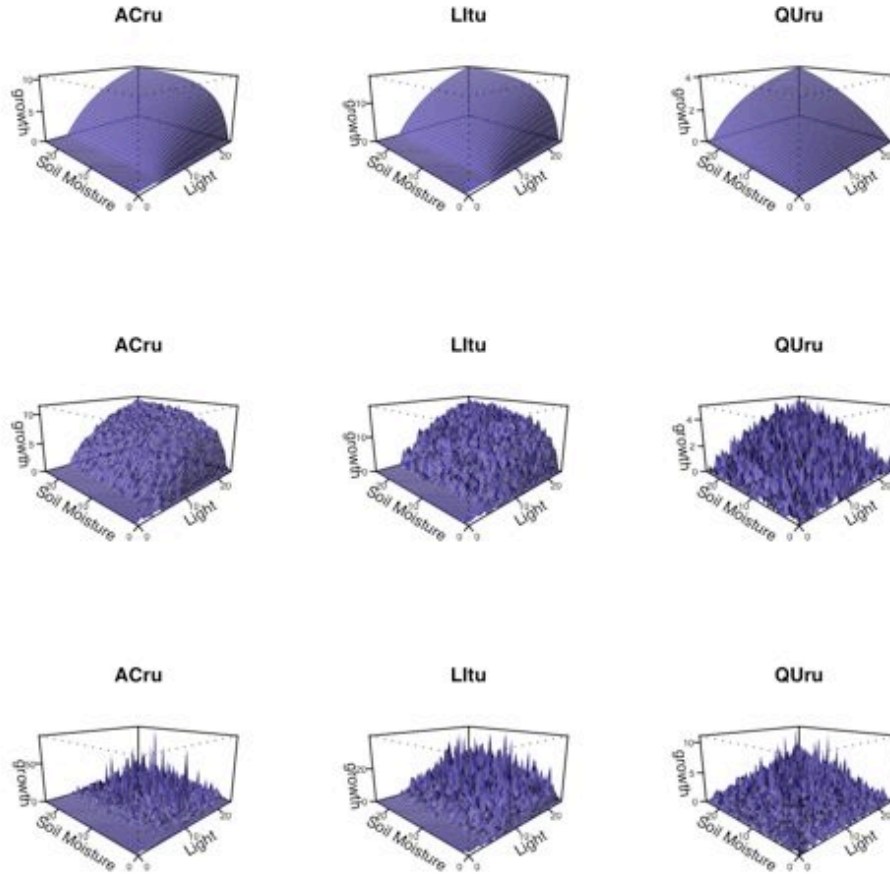
Figure 4. Example simulations of the response of seedling growth to soil moisture and light for three species: *A. rubrum, L. tulipifera, and Q. rubra*. The three rows show a) the deterministic relationship between covariates and growth, b) an instance where process error has been drawn for each individual from the process error distribution estimated from data, and c) where instances of individual effects as well as process error are drawn from their respective distributions. Error is represented by drawing random deviations from the error distributions, and therefore are *examples* of the uncertainty and not the actual estimated error terms in order to visualize the variance due to error.
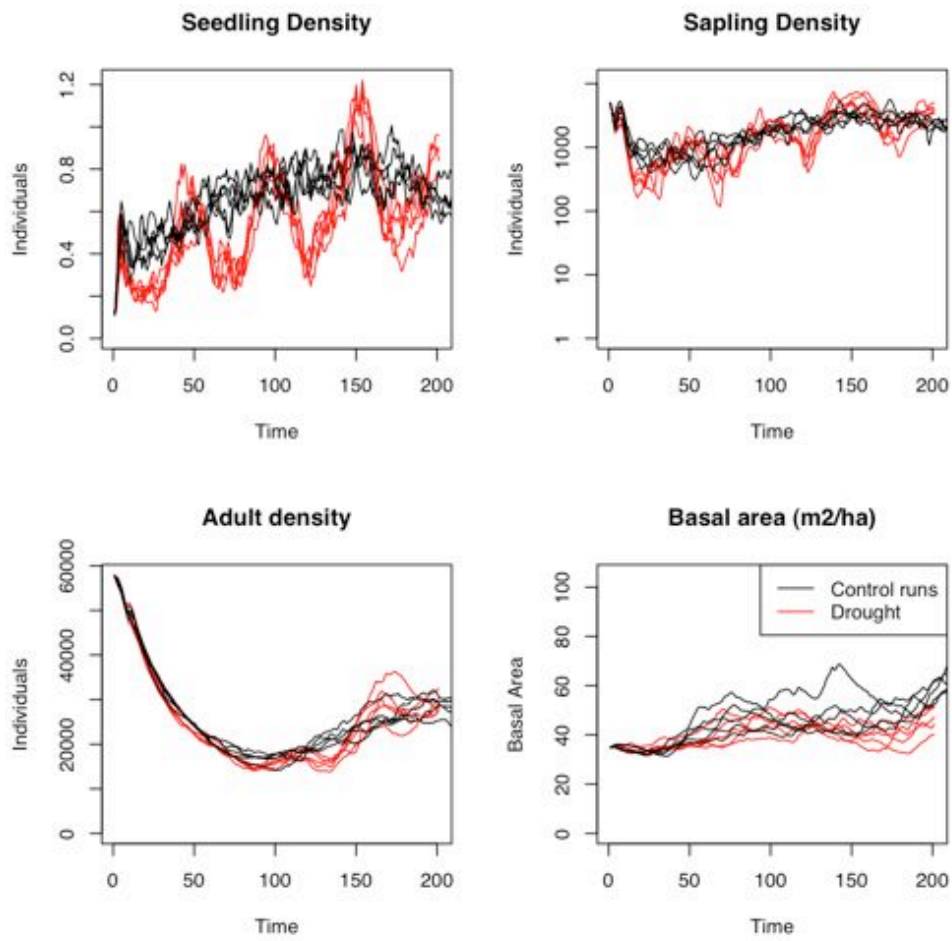
Figure 5. Time series for five separate 200 year simulation runs with drought treatments (red lines) and without (black lines). Note log y-axes for saplings.