

BioMove – an integrated platform simulating the dynamic response of species to environmental change

Guy F. Midgley, Ian D. Davies, Cécile H. Albert, Res Altwegg, Lee Hannah, Gregory O. Hughes, Lydia R. O'Halloran, Changwan Seo, James H. Thorne and Wilfried Thuiller

G. F. Midgley and R. Altwegg, *Climate Change Research Group, Kirstenbosch Research Center, South African National Biodiversity Inst., P/Bag x7, Claremont 7735, Cape Town, South Africa.* – I. D. Davies, *Fenner School of Environment and Society, Australian National Univ., Canberra ACT 0200, Australia.* – C. H. Albert and W. Thuiller (wilfried.thuiller@ujf-grenoble.fr), *Laboratoire d'Ecologie Alpine, UMR-CNRS 5553, Univ. Joseph Fourier, BP 53, FR-38041 Grenoble Cedex 9, France.* – L. Hannah, *Conservation International, Bren School of Environmental Science and Management, Univ. of California, Santa Barbara, CA 93106-5131, USA.* – G. O. Hughes, *ADAS Environment Group, Woodthorpe, Wergs Road, Wolverhampton, WV6 8TQ, UK.* – L. R. O'Halloran, *Dept of Zoology, Oregon State Univ., Corvallis, OR 97331 USA.* – C. Seo, *Dept of Geoinformatics, Univ. of Seoul, Seoul 130-743, Korea.* – J. H. Thorne, *Dept of Environmental Science and Policy, Univ. of California, Davis, CA 95616, USA.*

BioMove simulates plant species' geographic range shifts in response to climate, habitat structure and disturbance, at annual time steps. This spatially explicit approach integrates species' bioclimatic suitability and population-level demographic rates with simulation of landscape-level processes (dispersal, disturbance, species' response to dynamic dominant vegetation structure). Species population dynamics are simulated through matrix modelling that includes scaling demographic rates by climatic suitability. Dispersal functions simulate population spread. User-specified plant functional types (PFTs) provide vegetation structure that determines resource competition and disturbance. PFTs respond annually through dispersal, inter-PFT competition and demographic shifts. BioMove provides a rich framework for dynamic range simulations.

One of the core needs in conservation biology is the assessment of the long term viability of populations of a species under a range of possible management interventions and environmental changes. Several approaches for assessing population viability have been proposed and implemented. These population viability approaches (PVA) provide a useful tool to assess population viability in a given context (Lacy 1993). However, climate change that is likely to cause changes in species home range and in population sizes within home ranges, minimizes the value of these approaches as they are currently designed (Thuiller et al. 2008). They are usually not spatially explicit and do not include the direct effect of climate change on demographic parameters. They also ignore the interactive dynamics between environmental change and landscape process (e.g. succession, shift of biome boundary) and are often difficult to parameterise for a large number of species.

Alternatively, landscape models have been traditionally used to explore the influence of disturbances on vegetation dynamics and look for emerging patterns over long time spans (e.g. hundreds of years, Baker 1989). They typically do not focus on one subject species. Rather, they address biotic interactions between groups of species commonly called plant functional types that represent

different components of a community (Albert et al. 2008). Landscape models explicitly focus on processes such as dispersal, fire and human disturbances, and for this reason include simplified representation of the demography and biotic interactions. These simplifications of vegetation dynamics are essential to represent landscape processes where local-scale processes are over-ridden by larger-scale disturbances and where habitat suitability is expected to be constant. For this reason, they are traditionally not used in a climate change context.

Finally, climate impact assessments on species are mostly carried out with habitat suitability models characterising the suitability of a given environment for a species, based on climate and other inputs (such as soil type or land cover) (Heikkinen et al. 2006). These approaches allow climate change driven spatial shifts in species suitability to be mapped. While these attempts can explore impacts on a wide range of species, and thus provide useful, even if preliminary, estimates of risk of extinction for endemic faunas and floras, they are criticised for a range of reasons. Firstly, they derive the likelihood of occurrence in any particular site by correlating occurrence data with selected environmental variables – an approach that has been much discussed and is currently considered pragmatic but

problematic (Dormann 2007). Secondly, they do not realistically account for population-level processes especially at the leading and trailing edges of geographic ranges, including dispersal and establishment of populations in new geographic ranges and persistence in sub-optimal conditions. Thirdly, they are blind to community interactions (e.g. competition) and disturbances (e.g. fire or grazing).

The models described above all offer unique contributions to conservation biology modelling. We propose here that a hybrid approach, combining the advantages of PVA approaches, landscape models and habitat suitability models, would permit more realistic estimates of potential population change rates. This would also allow the interactive effects of landscape dynamics and environmental changes to account for idiosyncratic changes that may be occurring throughout different parts of a species' home range (Keith et al. 2008).

Our proposition has led us to develop BioMove, a novel modelling tool designed initially to assess global change risk to species persistence. With its roots in ecological niche theory (Hutchinson 1957), BioMove couples landscape and population modelling to provide a more robust simulation of the demographic and community processes that affect persistence and realization in a newly available range. BioMove has been designed inside the LAMOS framework (Lavorel 2001) which uses plant functional traits to integrate different ecological processes operating at the landscape scale. Within each pixel of a geo-referenced grid, community dynamics are modelled by applying a succession model that uses demographic, regeneration and morphological traits at the functional type or species level. BioMove is implemented as a succession model in LAMOS and uses its dispersal and

disturbance methods. We believe BioMove offers a novel approach in that it provides a method to simultaneously model plant function types (PFT) that determine vegetation structure and the demography of particular species with regard to dynamic habitat suitability in response to environmental and landscape changes (Fig. 1).

To model the vegetation dynamics, BioMove uses a modified version of the FATE succession model (Moore and Noble 1990). It is relatively easy to parameterise with the knowledge of field biologists and relevant data from the current literature. The PFTs are chosen based on their relevance to the ecosystem studied and the ecological questions at hand. For instance, to investigate the ability of the European larch to colonize semi-abandoned sub-alpine grasslands, Albert et al. (2008) defined four leaf-height-seed (LHS)-based PFTs, classifying the dominant graminoids in contrasting nutrient economies and competitive effects and responses after Westoby's (1998) LHS plant strategy scheme and one tree PFT representing the larch. These four grass PFTs and one tree PFT were sufficient to represent the vegetation structure of the study area. In another study, Hannah et al. (2008) used BioMove to simulate the interaction of a pine species, *Pinus lambertiana*, with a single PFT representing the oak-dominated vegetation expected to displace the pine under climate change.

BioMove requires semi-quantitative parameters to simulate the PFTs, including their competitive ability at different life stages, their dispersal ability (via both short and long distance dispersal functions), their mortality and regeneration responses to fire, grazing and other disturbances relevant to the study area (disturbance model). This information can be derived from literature, trait databases,

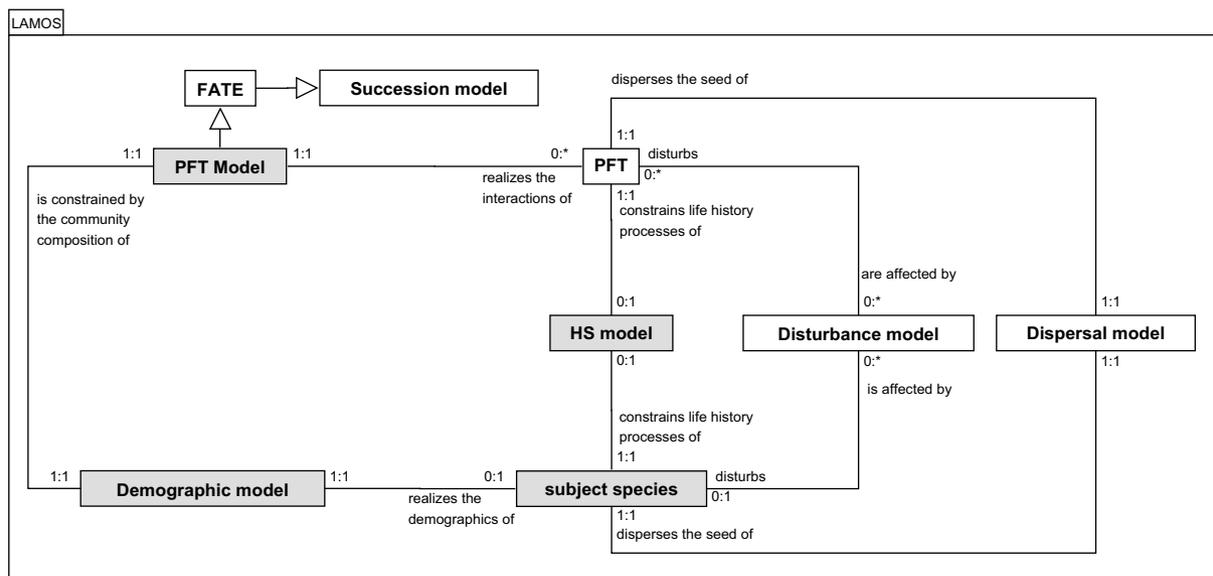


Figure 1. A conceptual UML class diagram depicting LAMOS configured with BioMove. Grey boxes are components comprising BioMove while the remainder are components already available in LAMOS. The components (boxes) their multiplicity and relationships (lines) can be read as a simple sentence. For example, “one PFT model realizes the interactions of zero or more PFT(s)”. Lines with arrowheads indicate generalizations or, read the other way, specializations. For example, the PFT model is a specialization of FATE. The multiplicities indicate that BioMove can be run as a single species demographic model (zero PFTs) or a multi-PFT community model (zero subject species) or both. In addition, constraints imposed by the HS (habitat suitability model) are optional (0:1). The number of disturbance models is also optional, that is zero or more disturbances can affect zero of more PFTs. The diagram stipulates that there is one dispersal model for each PFT.

field measures or expert knowledge. In its current configuration, only competition for light is simulated in the FATE model (Fig. 2 – PTF succession). The FATE module in BioMove handles the vegetation and seed pool dynamics by tracking annual cohort abundance for juvenile and mature age classes.

BioMove simulates the dynamics of a given plant species within this dynamic landscape. We believe this decoupling between species and PFTs is necessary as few models include biotic interactions and the resulting mosaic into the modelling of population dynamics. Spatially explicit models like Ramas GIS only constrain the size of populations by the carrying capacity of the subject species (Keith et al. 2008) but not by the light availability or the vegetation structure of the area. This coupling resolves most of the criticisms formulated against the use of meta-population models at regional scale and makes the estimation of extinction risks of endangered species more realistic.

To estimate uncertainty, LAMOS provides a script interface for the design and execution of multiple simulations. Data for any or all model variables can be exported in a variety of formats. In addition, a Monte-Carlo feature provides a means for generating such scripts to explore the model's parameter space. This includes implementation of a Latin Hypercube design where prior knowledge of parameter distributions around some mean and possible correlations between parameters may be used to limit the number of simulations to a tractable number.

BioMove uses a demographic model (Fig. 3) to simulate the dynamics of the subject species within the landscape, with key demographic rates. The demographic model is a mixed age/stage population demographic model implemented in each cell. Age is used to specify the juvenile age classes. Once cohorts achieve the sub-adult age class, transitions between sub-adult and adult age classes become probabilistic (Fig. 3). Different biological traits are necessary to parameterise this demographic model, such as (st)age-specific mortality and fecundity, age at maturity and disturbance response. Similarly, the dispersal characteristics of the species are also required (mean dispersal distance, fraction of seeds long distance dispersal). Our approach differs from animal population viability analysis (PVA) in only having undirected movement between pixels (kernel seed dispersal). Models of animal populations often have directed (intelligent) movement between patches. Different seed dispersal models can be added to LAMOS by modellers to provide for particular dispersal syndromes (van der Pijl 1982). This is an area of research we are currently pursuing with particular regard to the implications for modelling animal populations in BioMove.

The light availability resulting from the simulated landscape is then used inside the species demographic model to simulate the competition for light between the vegetation and the modelled species, depending on its shade tolerance at different life stages (germinant, immature and mature stage). This is a one way effect in the sense that the subject species does not influence the PFT composition in return (see below in the case of a dominant or invasive species).

We also introduce the ability to simulate the influence of environmental change on the dynamics of the vegetation structure and the subject species. What makes

BioMove unique is its coupling to habitat suitability models. The habitat suitability determination for each PFT and the subject species is performed outside of BioMove for the study area. We did not include this process inside BioMove as there are many techniques with different assumptions and we considered it important to allow user choice in the method applied (Marmion et al. 2009). The habitat suitability (HS) model can be estimated using climate-only data (e.g. in a climate change context), soil or any resource variable and then projected using the different climate change scenarios available. The output of this process is a single layer supplied to BioMove representing the HS (numeric value between 0 and 1) for a PFT or the subject species at some point in time. Many layers may be required to represent the dynamics of land use or climate change for a given scenario. These can be read into BioMove during a model run as directed by a script file. There is no fixed time step for this process. A set of HS layers represents a single land use/climate change scenario. A scenario can then be viewed as a parameter value and the uncertainty associated with a scenario measured in the same way as uncertainty in other BioMove parameters.

Once imported into BioMove, the HS is used to scale the demographic processes, mortality, recruitment and fecundity and has the effect of excluding recruitment of the species and PFT in unsuitable habitats (Keith et al. 2008). The scaling process and the form of the relationships between HS and the parameters are decided prior the simulations. If there is no information about the relationship a factorial design in implementing simulations is recommended to estimate the sensitivity of the species or PFT to this relationship. This approach has the potential to make the PFTs and subject species effectively variable with regard to environmental conditions. For example, morphological parameters and the timing of life stage events could be set to change with HS providing different competitive abilities between the PFTs (Fig. 2).

There are various potential applications of BioMove. At the regional scale, BioMove is useful for projecting vegetation dynamics in response to both climate and land use change. This is critical to evaluate the consequences of these dual factors to ecosystem functions and associated goods and services. Different scenarios can be envisaged according to various adaptation or mitigation plans, for example, forced growing or mowing to prevent bush encroachment (implemented as specific disturbances in BioMove). More specifically, it is highly relevant to investigate extinction risk of subject species in the face of climate change or/and land use change. Previous attempts have ignored biotic interactions and the influence of communities (Keith et al. 2008). To explore the effectiveness of proposed adaptation plans, specific corridors across protected areas can be simulated to investigate their usefulness in decreasing extinction risk.

Finally, with regard to the growing threats due to invasive species, BioMove could simulate the ecosystem modifications arising from an invasive PFT and the consequences this has for the species “at risk”, native community and ecosystem functions. Given the amount of money invested each year for alien species eradication, such a tool simulating the spread of invasive species through the landscape under different eradication strategies (e.g. implemented as specific

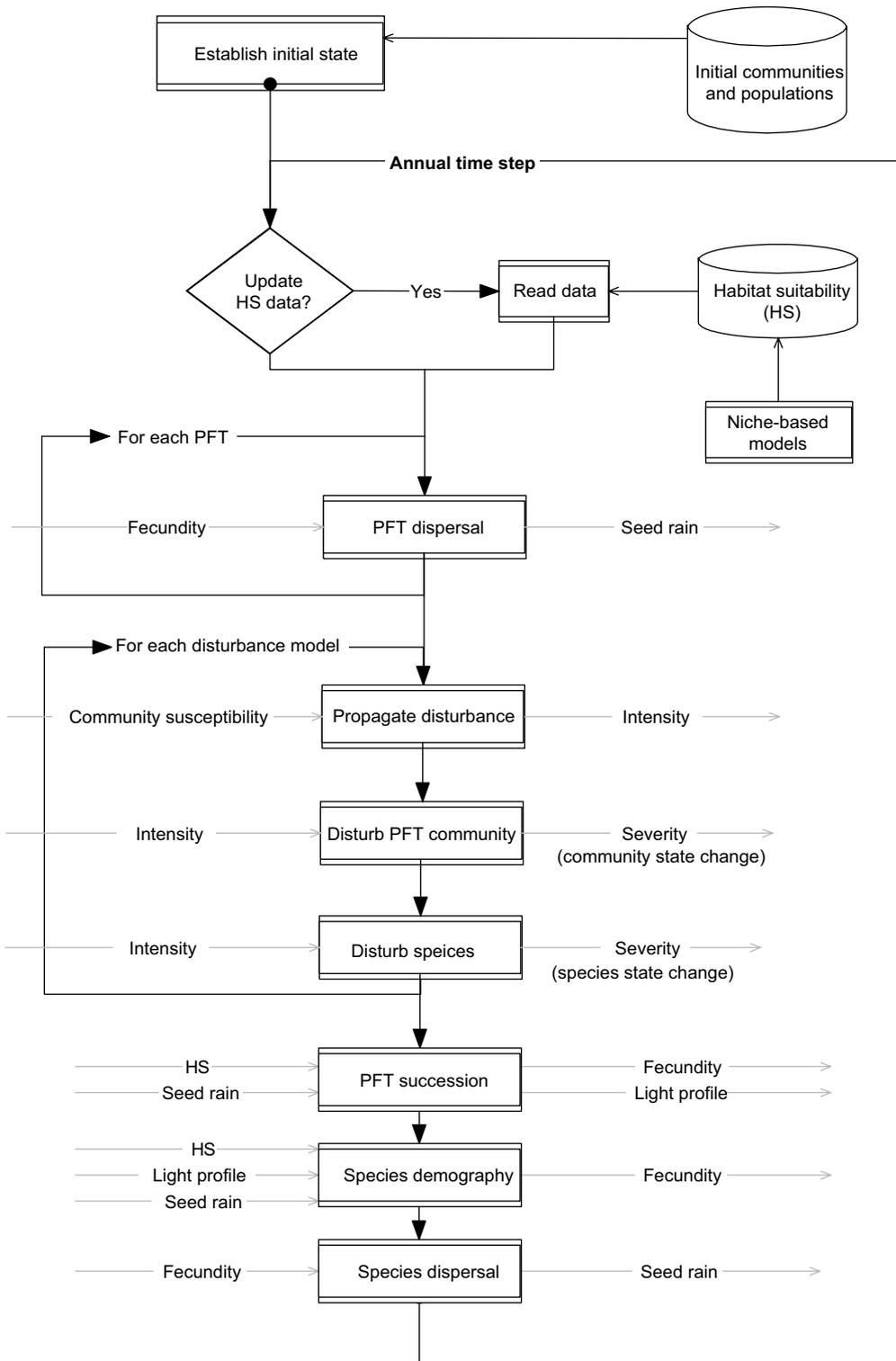


Figure 2. Flow chart of the principle sub-routines in BioMove. Solid arrow heads indicate the sequence of sub-routine calls. Horizontal arrows show the main inputs and outputs from each sub-routine.

disturbance) are of crucial importance to identifying management options that maximize ecosystem integrity while minimizing eradication costs.

Three key assumptions need to be born in mind when considering the appropriateness of BioMove to a research question. These three points are in regard to coupling

between various components of the model. Firstly, it is assumed that the habitat suitability can be established independently from BioMove simulations, that is, HS is determined by habitat suitability modelling techniques using exogenous variables such as climate, soils and topography. Secondly, it is assumed the population density

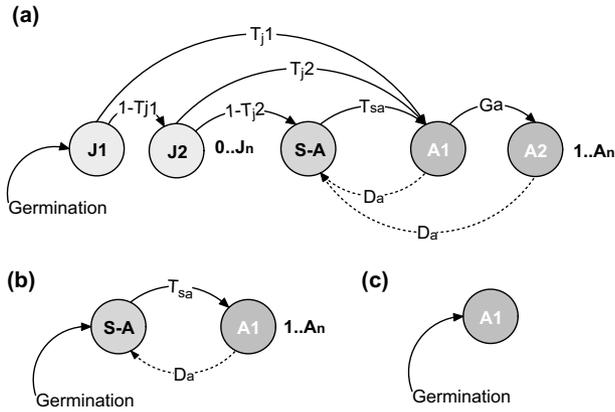


Figure 3. Transition paths for the BioMove subject species model. The simplest arrangement (a) is for germinants to recruit directly to the adult age class as is the case for annuals modelled with a yearly time step. The next level of elaboration (b), is to have a single sub-adult age class to provide the opportunity to delay seed production for adults after disturbance. Beyond this, any number of juvenile and adult age classes can be added. G_a is the transition probability between adult age classes (growth rate). The default value for T_j (juvenile maturation rates) is zero which results in a time of arrival at the sub-adult class equal to the number of juvenile age classes. To model annuals (c), the single adult age class has a mortality rate of 1 (not shown). D_a is the transition from adult to sub-adult caused by disturbance (re-sprouting).

of the subject species is sufficiently low so as not to have any competitive effect upon the PFT community. The coupling is unidirectional. This is a reasonable assumption given that one of the purposes of BioMove is to examine the viability of populations at risk rather than robust populations in high abundance, but fails when a subject species drives processes itself, as discussed below. Thirdly, the disturbance regime is influenced only by the PFT(s), and not by the population size of the subject species. It is the community mix of PFTs that provides fuel or food for disturbance models within LAMOS. This is also a reasonable assumption given the second point above. However, this potentially limits BioMove for the application of modelling keystone species that may cause switches in ecosystem structure and function, such as invasive aliens. In such a case we suggest that the subject species are best modelled as a PFT in the community model rather than a low density population in the demographic model.

BioMove is written in the Delphi (v. 7) programming language and incorporated within the LAMOS platform through recompilation. The software, source code and documentation are free and available from http://purl.oclc.org/NET/amos_biomove.zip. To modify BioMove, it will be necessary to obtain and install Delphi; Abbrevia, XStringgrid (both freeware from sourceforge.net) and TeeChart (commercial). BioMove has been tested on Windows 2000 and XP. Disk space required for the download files is 60 Mb. Memory requirements for a simulation with 10 000 cells and four PFTs is 23 Mb and takes 1 min to run 100 time steps (yr) on a current model desktop computer. LAMOS places no constraints on spatial grain or extent, however, grid sizes greater than 10^7 pixels are a practical

upper limit. Some elements of BioMove are stochastic and LAMOS provides features to manage replicate simulations.

To cite BioMove or acknowledge its use, cite this Software note as follows, substituting the version of the application that you used for “Version 0”:

Midgley, G. F., Davies, I. D., Albert, C. H., Altwegg, R., Hannah, L., Hughes, G. O., O’Halloran, L. R., Seo, C., Thorne, J. H. and Thuiller, W. 2010. BioMove – an integrated platform simulating the dynamic response of species to environmental change. – *Ecography* 33: 612–616 (Version 0).

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