

Having your cake and eating it: A modelling framework to combine process-based population dynamics and dispersal simulation

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Abstract: This paper will introduce and demonstrate the capabilities of the newly extended ‘Spatial DYMEX’ model software. Spatial DYMEX allows modellers to develop process-based population dynamics simulations that include spatially-explicit dispersal. Traditionally, models of species dynamics have focused on either population demographics or dispersal processes. Where trade-offs in model detail between processes describing population dynamics and dispersal have frequently been required, Spatial DYMEX utilises a computationally-efficient cohort-based approach that allows the model to capture both temporal and spatial population variability. The computational efficiency results from the professionally developed underlying code structure and re-usable modules that allow the modeller to rapidly develop models without knowledge of computer code. Cohorts are a single entity that is used to represent a well-defined group of individuals who share the same or similar characteristics (e.g. of the same age and sex) who are studied over a period of time. They are commonly used in ecological modelling.

DYMEX includes a graphical user interface that employs conceptual modules that are familiar to ecologists (e.g. lifecycles) and combines them with a library of customisable mathematical functions (e.g. logistic). Multiple lifecycles can be included in a model, and they can be linked to simulate a variety of ecological interactions (e.g. predation or competition). Deme structures can be used to include the effects of genetic diversity, for exploring topics such as pesticide resistance. Spatial DYMEX includes a range of graphical and spatial visualisation tools to analyse model outputs.

This novel modelling software allows the modeller to capture simultaneously the dynamics of spread with a consideration of the ecological, environmental and behavioural factors that precede a migration or dispersal event and the consequences of dispersal. We demonstrate the capabilities of the enhanced Spatial DYMEX package using a case study of the population dynamics and dispersal of an aphid-virus-wheat system. The mechanistic, cohort-based approach offered by DYMEX allows us to simulate how various environmental drivers may impact upon processes that drive wheat growth and aphid (*Rhopalosiphum padi*) population dynamics, allowing us to estimate potential outcomes under future climate scenarios. A driving question for this research is whether Yellow Dwarf Virus, which is spread by aphids, will become a greater threat to wheat yields under climate change. The spatial modelling capabilities of the latest DYMEX now allow us to examine the spatial implications, where shifts in the timing of migration events at the start of the season may alter the timing of arrival and subsequent population dynamics of the aphids and virus in the wheat crop.

Keywords: DYMEX, Spatially-explicit modelling, Model development software, Dispersal

1. INTRODUCTION

Many pests, diseases and weeds are mobile or migratory. For such species, economically important applications such as biosecurity risk assessment, pest alert systems, pest management and forensic investigations of biological incursions, are complicated by the need to consider both the phenology and dispersal of the pests in addition to their habitat suitability in space and time (Jongejans *et al.* 2008; Savage *et al.* 2010). Long-distance transport of organisms through the atmosphere, oceans, and via human-mediated vectors are important modes of transport for pests and pathogens (Munoz *et al.* 2004; Gilbert *et al.* 2005; Kim & Beresford 2008; Robinet *et al.* 2009; Chapman *et al.* 2010; Hopkinson & Soroka 2010). The factors affecting the direction and velocity of movements may be temporally sensitive or significantly stochastic in nature. Therefore, when considering such movements, it is important to consider the timing of migration or dispersal from spatially-explicit source populations, as well as the transportation process itself. Many studies have only focused on part of this process; perhaps simply mapping migration pathways (Scott & Achtemeier 1987), rather than considering the environmental and behavioural factors that precede or elicit a migration or dispersal event (Holyoak *et al.* 2008). The reason for this is the lack of suitable integrated tools to simulate phenology and dispersal at the same time. Where there is a need for accurate immigration models, population dynamics models are presently typically loose-coupled to dispersal models e.g. the DYMEX – PMTRAJ model of the Australian Plague Locust (Deveson *et al.* 2005), or rely upon field observation data to initiate the dispersal model (Hopkinson & Soroka 2010).

Recent advances in data management and processing now allow for wind trajectory models to be coupled with ecological models of population dynamics – allowing modellers to simulate both processes mechanistically in the same model framework. This enables a population dynamics model to be easily spatialised (i.e. to have your cake and eat it)! Meteorological data availability, modelling techniques and knowledge about ecological behaviours have also improved, allowing for a more integrated approach (Chapman *et al.* 2010). In this paper we describe how the DYMEX population modelling system was extended to better support simulations of spatio-temporal population dynamics through the tight integration of a generic process-based population dynamics model with a dispersal model. The resulting system is demonstrated with an example of a tri-trophic wheat-aphid-virus system. Due to ongoing development of the latest DYMEX the examples presented here are taken from a loose-coupled version, which combines the population dynamics simulations in DYMEX run on Windows with an existing trajectory model (PMTRAJ) run on Linux.

2. SPATIAL DYMEX

When studying the population dynamics of a mobile species, it is virtually impossible to remove the species from its spatial context (site-specific weather patterns, lithology, disturbance patterns, biotic context and dispersal sources and sinks etc.). Therefore, to construct process-based simulations of the impacts of environmental change on mobile organisms, the DYMEX modelling software has been extended to better support spatially-explicit simulations, including wind dispersal. To illustrate this, we have used Spatial DYMEX to model the impacts of climate change on the aphid *Rhopalosiphum padi* – a highly mobile and migratory insect pest. A mechanistic approach is necessary when studying the potential impacts of climate change on a tri-trophic system such as aphid-wheat-virus so that multiple effects of changing climatic variables on biological processes can be captured. Such subtle processes and system feedbacks are not captured by simpler demographic models.

The DYMEX package aims to help ecologists overcome the computing difficulties associated with constructing a simulation model, allowing them to build mechanistic, process-based models without the need to learn complex computer programming skills (Maywald *et al.* 2007). The two components of DYMEX are a model Builder and a Simulator. The model is created and modified with the Builder software, then the model is run using the Simulator software, which displays results of the simulation including charts and tables. DYMEX provides ecologists and biologists with a user-friendly system to build population dynamics models spanning the full range of complexity, from the simplistic to highly detailed metapopulation dynamics models to explore climate change impacts (Kriticos *et al.* 2003) and multi-trophic models of weed biological control systems (Kriticos *et al.* 2009) and pest population dynamics (Yonow *et al.* 2004).

In DYMEX Version 3 (Maywald *et al.* 2007), initialisation and processes describing dispersal between spatial cells had to be specified manually for each source cell. This limited the spatial complexity that could practically be included in a model. In the new version of DYMEX, spatially-explicit simulations are facilitated by the use of ThinkGeo Mapsuite <http://gis.thinkgeo.com/>, which provides a spatial database, combined with a simple customised Geographical Information user interface. This allows the user to zoom to an area and specify a simulation grid, as well as to view and upload spatio-temporal data (ascii or arcgrid format) to the database. Spatial or spatio-temporal data is then made available to a model via an enhanced database module. This database is then imported into the simulator and linked with the model description file.

DYMEX operates spatially by running multiple instances of a population dynamics model in each cell of the spatial grid that is specified by the user (figure 1). DYMEX 3 could only handle a single population (P) in a model. Although adding Demes in DYMEX 3 allowed for sub-populations with cohort separation and re-connection (e.g. to represent genetic diversity), Demes were not previously spatially explicit. The Deme structure has facilitated the implementation of Spatial DYMEX by the creation of ‘spatial’ Demes (i.e. spatially-explicit sub-populations), so that $P_{total} = P_1 + P_2 + P_3 \dots P_n$ (where n = number of grid cells in the selected model region). Spatial DYMEX permits migrants from a cohort to move across the simulation space to establish or join another cohort in a new grid cell. At present the movement module in Spatial DYMEX is implemented as a mechanistic model of dispersal by wind, ‘PMTRAJ’ (Dillon *et al.* 1996). This was because the aphid case study required a model of movement that handles long distance wind vectored migration. In future a range of movement modules with different drivers can be added to Spatial DYMEX. PMTRAJ requires global input parameters relating to the flight behaviour of a species, including take off time and duration, flight height and duration, flight speed and offset against the wind (if the organism is able to fly against the wind). PMTRAJ also requires spatial multi-level wind data, such as LAPS (Albers 1995). The modular approach to building DYMEX means that in the future, other dispersal models can be included with minimal additional coding required to specify inputs, outputs and run parameters required for each model option.

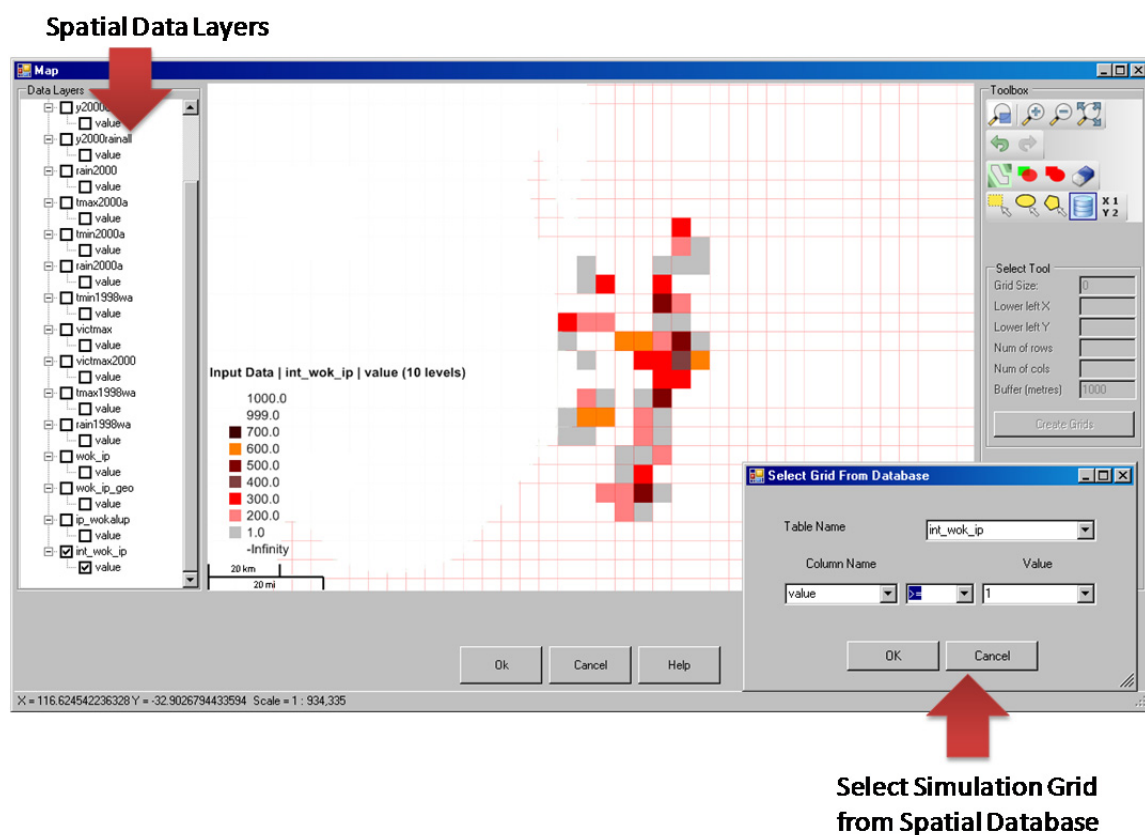


Figure 1: Screenshot of Spatial DYMEX Map viewer, showing aphid population source grid (hectares of irrigated pasture) and geodatabase grid selection tool.

3. CASE STUDY: APHID-VIRUS-WHEAT SYSTEM IN WESTERN AUSTRALIA

3.1. Model structure

We developed a model using Spatial DYMEX to simulate the impacts of the aphid-wheat-Yellow Dwarf Virus (YDV) pathosystem on potential wheat production under historical and future temperature, rainfall and atmospheric CO₂ levels.

In Australia, the cereal aphid *Rhopalosiphum padi*, commonly known as the Bird Cherry-oat Aphid, damages crops by spreading Yellow Dwarf Virus (YDV). A case study of a major wheat production area in Western Australia (Avondale) (figure 2) was modelled to assess the regional effects of climate change on the yield of wheat in the presence of the aphid and virus. This region was chosen since a number of previous field studies of aphid population dynamics were available to compare with simulation results in 1998-2001 (Thackray *et al.*

2009). Asexual populations of aphids disseminate the virus in Australia through continuous cycling and transmission from perennial pasture and both native and introduced grass species to annual crops such as wheat and barley. The cycle varies between climatic zones, as some regions have more suitable grassland reservoirs over summer than others (McKirdy & Jones 1993). For example, the drier region of South-western Australia generally relies on irrigated pasture and roadside grasses as a source of aphids migrating into the autumn crops, whereas further east, perennial and natural grasses provide a reasonable source of aphids when there is sufficient rainfall (De Barro *et al.* 1992; McKirdy & Jones 1993). In this case study we focus on the distinct potential source of aphids from irrigated pasture to the west, particularly from a large area of irrigated pasture around Wokalup. However, we acknowledge that other sources of aphids are likely to exist in this landscape such as roadside grasses in the crop region and native grassland in the south. Land use in the simulation was defined using ArcGIS 9.3 (ESRI, Redlands, California) as a set of 5 km × 5 km cells coded as irrigated pasture, wheat cropping, or unsuitable.

Other assumptions in the model include the assumption that wheat cells contain no aphids at the time aphids arrive in the crop and that we represent within-cell dispersal using a simple exponential function model (after Kendall *et al.*, 1992 and Thackray *et al.*, 2009). We also assume that wind speed and direction are unaffected by climate change. These assumptions are as yet untested for their impact on the model.

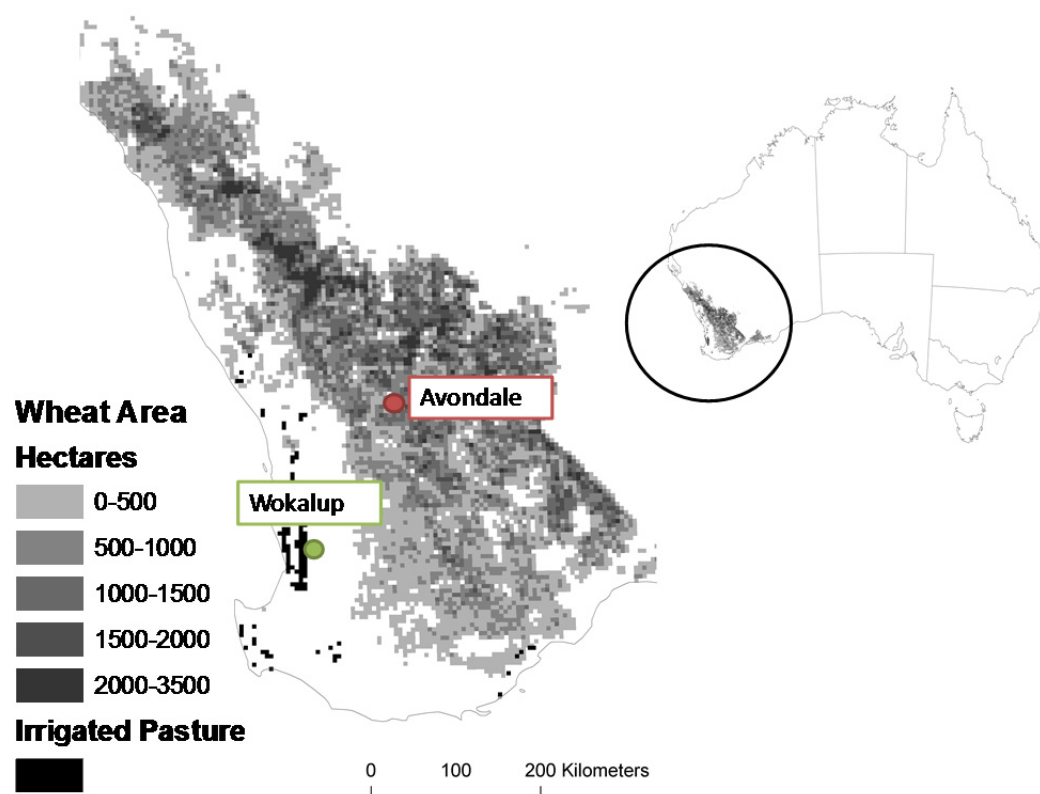


Figure 2: Case study region, Avondale and Wokalup, Western Australia.

The integrated spatial model (figure 3) is run on a spatial grid, with data layers for variables such as temperature, rainfall and land use. The timing of migration is driven by the aphid simulation model in the irrigated pasture cells, incorporating alate formation and subsequent aphid migration events. When appropriate, aphids migrate from cells in the irrigated pasture zone and disperse according to the wind fields prevailing immediately subsequent to the time of dispersal. Migrating aphids that disperse into cells containing wheat either establish new cohorts, or are combined with other cohorts if rules defining similarity of life history are satisfied. If they disperse into unsuitable habitat they are immediately killed. The flight duration and direction is determined by the dispersal module in Dymex (presently limited to PMTRAJ, or a user-defined spatial rule). We chose one such cell at Avondale, WA, to initiate the model in the wheat field at that location according to aphid landing densities simulated by PMTRAJ. We looked at the simulated aphid population dynamics over time, as well as wheat growth and the consequences of aphid arrival for YDV virus spread within the cell.

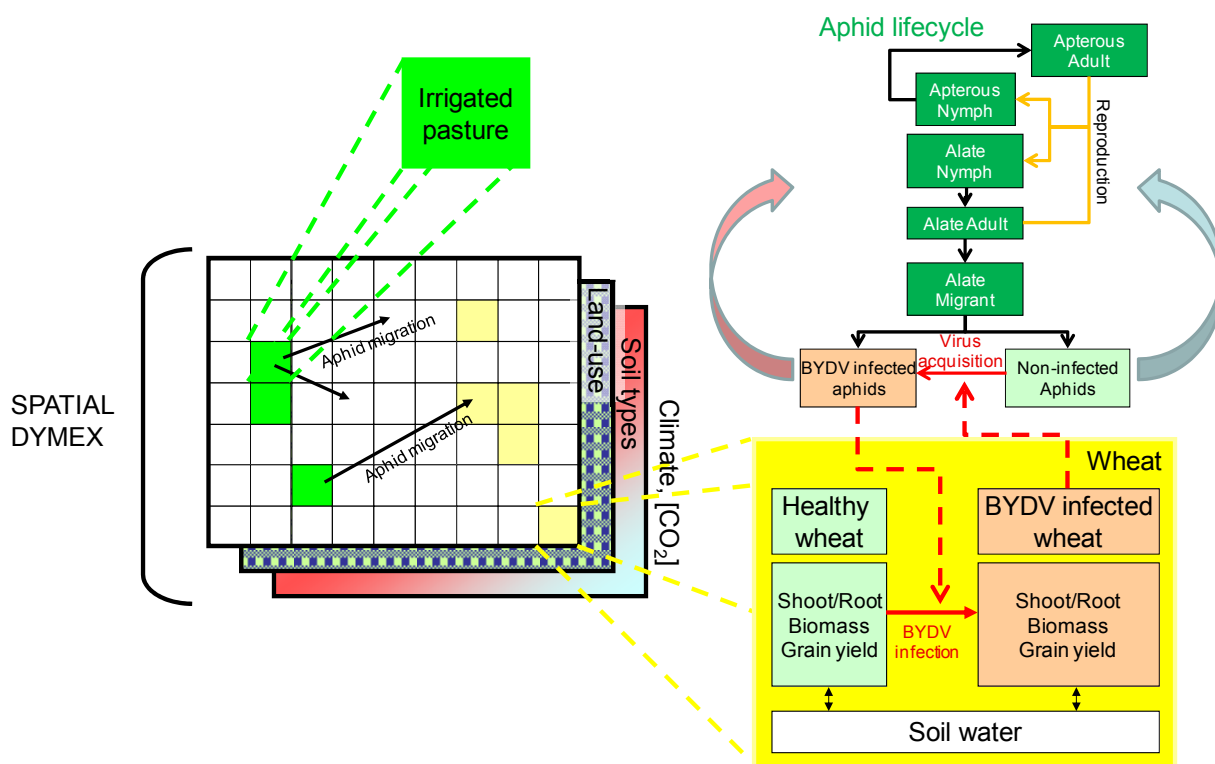


Figure 3: Aphid-Wheat-Virus model overview diagram

3.2. Results

Our preliminary findings suggest that this pathosystem may become a lesser problem for the grains industry in this region under future climates (2030 and 2070 horizons). Migrating populations of aphids from grasslands are likely to arrive later into the crop under future climate scenarios. However, as crop and aphid development both advance faster under future climates, the result will be more rapid aphid population growth in the early part of the season and earlier “in-crop” alate (winged) formation under future climates. Without YDV, yield is expected to decline under future climates. This assumes that current wheat management practices will continue (same sowing date, wheat varieties and a good supply of nitrate fertilizer). Furthermore, the proportional impact of YDV on grain yield is expected to decline under future climates (figure 4). In the short-/mid- term (2030 scenario) the rate of spread of YDV is also expected to decline, however YDV outbreaks in 2070 may spread faster, according to the model (figure 5). The increased rate of spread is driven by early alate formation in the crop in 2070. Whereas the effect of YDV on yield and growth of the crop responds to the timing of infection in relation to crop growth stage, as shown by our experimental work that is underpinning these model results.

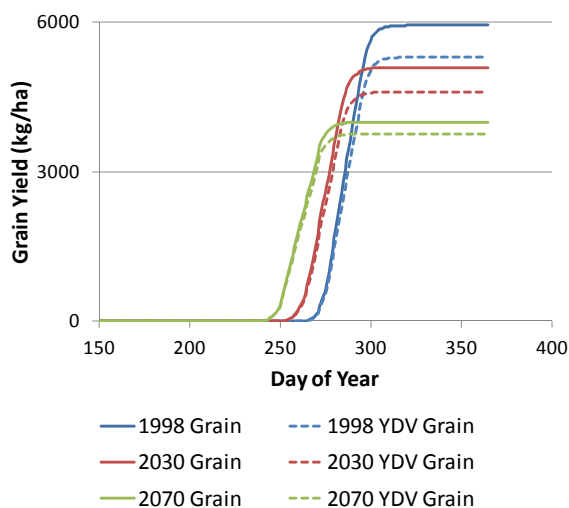


Figure 4: Comparison of YDV infection rate in crop through time, 1998 compared to future climate scenarios.

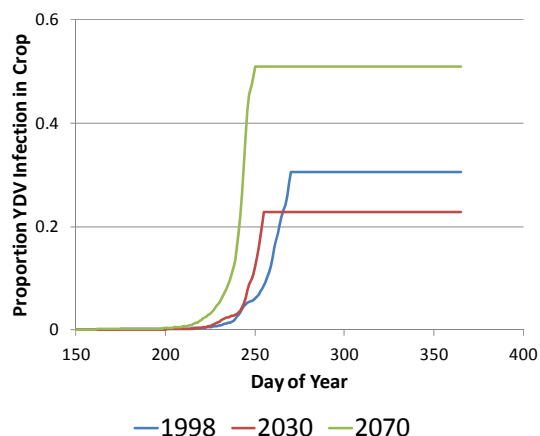


Figure 5: Comparison of YDV infection rate in crop through time, 1998 compared to future climate scenarios.

4. CONCLUSIONS AND RECOMMENDATIONS

The Spatial DYMEX modelling environment has been developed to simulate the modelling of dynamic spatio-temporal processes and its modelling interface can be used to interpret and analyse results. The Spatial DYMEX environment was also developed so that the outputs from its simulations, such as the modelled interactions of wheat/aphid/YDV under climate change conditions, could be communicated easily to stakeholders. Its data export function allows it to produce datasets in asciigrd format, which can be directly used by the previously developed geo-processing scripts and therefore visualised in the Google Earth environment. The development of this novel modelling environment represents a significant increase in our capacity to simulate the population dynamics of organisms across heterogeneous landscapes through time. Whilst integrated models of spatio-temporal population dynamics may find applications for better understanding the ecology of migratory species such as the monarch butterfly (Zalucki *et al.* 2004), the majority of their applications will probably lie in addressing a diverse range of economically important applications in invasion biology: biosecurity risk assessments, near-real-time pest alert systems, pest and disease management (including weeds) and forensic investigations of pest incursions.

The extended version of DYMEX allows ecologists studying and modelling long-distance dispersal to simultaneously consider and model the pre-takeoff state of migratory populations, such as their physiological age and stage profile and phenological cues for movement. This process-based tool will enable new types of questions to be addressed, and old questions to be addressed differently, perhaps providing novel insights into long distance dispersal and transport processes. An example of such novel questions is given here, by assessing the future impacts of climate change on the existing pathosystem of aphid-wheat-virus using a mechanistic modelling approach. These novel insights may be valuable in terms of both understanding historical migration events and projecting into the future to study possible changes to migration pathways. Comprehensive environmental, meteorological and ecological datasets will be necessary to drive these models, some of which may already exist and others may be identified through model development.

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