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Progress in DGVMs: a comment on “Impacts of trait variation through observed trait–climate relationships on performance of an Earth system model: a conceptual analysis” by Verheijen et al. (2013)

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Dynamic Global Vegetation Models (DGVMs) are now central elements in Earth system models and our ability to understand past and anticipate future changes in the Earth system is intimately linked to the quality of DGVMs (Prentice et al., 2007). There are many ways in which DGVMs need improvement and there are many exciting initiatives under way. In a recent manuscript Verheijen et al. (2013) describe one pathway. To provide context for their work they compare their approach to other initiatives. In this contribution we wish to point out ways in which Verheijen and colleagues misrepresented the aDGVM2 (which they incorrectly call the aDGVM, which is in fact a different model published by Scheiter and Higgins, 2009) as presented by Scheiter et al. (2013). While the aim of this piece is primarily to set the record straight, we additionally point out similarities and differences between the approach described by Verheijen et al. (2013) and that described by Scheiter et al. (2013).

Verheijen et al. (2013) motivate their study by stating in reference to JeDi-DGVM (Pavlick et al., 2013) and aDGVM2 (Scheiter et al., 2013) that “none of the approaches so far tried to maximally include trait variation based on observational trait data and capture multiple sources of this variation by relating trait data to environmental variables”. Although we appreciate that this statement was designed to illustrate the uniqueness of Verheijen et al. (2013) and the statistical approach they adopt, it does have the side-effect of suggesting that these two papers ignored variation in traits and the relationships between traits and the environment. We would like to point out that Fig. 5 of our paper plots the positions of modelled individuals in multivariate trait space and relates the axes of this trait space to environmental variables. In the same paragraph the authors go on to suggest that DGVM modellers need to apply assembly theory to better understand and model relationships between traits and the environment. This is exactly what we propose in Scheiter et al. (2013) where the introduction explicitly proposes that DGVM modelling could benefit from two branches of community ecology, namely coexistence theory and community assembly theory. Moreover the title of Scheiter et al. (2013) includes the words “learning from community ecology”. Our impression from reading Pavlick et al. (2013) is that the traits that

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JeDi-DGVM predicts at a site are, as is the case with aDGVM2, a function of how environmental attributes select for trait combinations. This is an interpretation that Verheijen et al. (2013) appear, in apparent contradiction to their statement we cite above, to share in their discussion when they state that “some DGVMs also implement the concept of environmental filtering, like the JeDi-DGVM Pavlick et al. (2013)”.

JeDi-DGVM (Pavlick et al., 2013) is further criticised because its traits are “not-measurable”. While we cannot assess what is measurable, we like to point out that invitingly measurable traits are not inherently more useful than traits that can be inferred using inverse statistical methods (see Hartig et al., 2012 for an overview of using inverse methods in the context of DGVMs).

At a prominent point in the discussion Verheijen state that the “aDGVM has not been validated with observational data”. This dismissive statement serves as invitation to the reader to ignore the aDGVM2. This is a curious criticism of our work, because we never claimed the aDGVM2 to be validated; the paper in question was explicitly a methods and concept paper and we did not make any forecasts. Furthermore, we are sure that most authors of DGVM models would not claim to have authored validated models. At best a DGVM model can claim to have passed some benchmarks, to provide a better benchmark score than competitor models. Furthermore, should an author pronounce a model “validated”, this pronouncement is not universal, but restricted to the domain of that study. This criticism is even more curious considering that the authors themselves at the conclusion of the introduction state that their study is not aiming to produce “realistic results” and that their focus lies in “evaluating the importance of incorporating climate-driven trait variation”. This disclaimer seems ad hoc given that considerable space in the manuscript is devoted to benchmarking the model and explaining why the benchmarks used might undervalue the performance of their modelling approach (e.g. “Our simulations with 7 vegetation classes performed less well, but this might partly depend on the chosen vegetation map” and “This implies that the estimates of GPP by Beer et al. (2010) might be too low”); space, that could have been used “evaluating the importance of incorporating climate-driven trait variation”. Perhaps the disclaimer was

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conservation of mass principles and mechanical constraints implemented in the model (Scheiter et al., 2013). Once trade-offs are defined, the actual trait values a plant may adopt in an aDGVM2 simulation are the outcome of trait filtering. We use the term “trait filtering” as shorthand for how the ecological processes implemented in the model define the trait combinations that persist in a simulation (Figs. 2 and 4 in Scheiter et al., 2013). A constructive criticism of Scheiter et al. (2013) would involve pointing out whether important trade-offs are missing from the aDGVM2 or if trade-offs included are mis-specified.

A further difference is that Verheijen use statistical smoothing methods to estimate how the three traits that are congruent between the JSBACH model and the trait databases vary in environmental space and then use the resulting functions as a lookup table to reparameterise every simulation year, for each grid cell, the traits of each plant functional type. In this context they criticise aDGVM2, stating that in the aDGVM2 “environmental filtering only acts on trait values through the next generation”. This is not entirely correct. The aDGVM2 allows thousands of individual plants, each with their own potentially unique set of traits, to exist in a simulated vegetation patch. These individuals can die at any modelled time-step as influenced by disturbance, competition and resource availability. In addition, other individuals with potentially novel trait combinations can germinate each year. As a consequence of these birth and death processes the community trait matrix will change every modelled time step. Furthermore, in the aDGVM2 we make a distinction between traits (inherited attributes) and phenotypes (the outcome of interactions between an organisms’ traits and its environment). Traits of a modelled individual cannot vary in the lifetime of that individual, but a modelled individual’s phenotype can change as it grows and is subjected to disturbance. In summary, the phenotypes of individuals are modelled to change each simulation time step and the community trait matrix changes every time an individual is born and every time and individual dies. It follows that the criticism that the aDGVM2 approach is flawed because it does not allow “traits” to vary between years is distracting and without substance.

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A related problem with using statistical methods to parameterise functional diversity in DGVMs is that the dimensionality of the parameterisation task is high. The Verheijen et al. (2013) approach essentially requires a different parameterisation for each time step, for each geographic location, for each plant functional type. Even though using correlations between environmental factors and traits is used to reduce the dimensionality of the task, many parameters are needed. A side-effect of this large number of parameters is that it provides the modeller with the flexibility to tune the model to a benchmark. As we discuss in Scheiter et al. (2013), one advantage of our method of combing trade-offs and trait filtering is that the dimensionality of the functional diversity parameterisation does not change with the number of functional types or with the number of geographical locations simulated.

A further reason why we would not advocate Verheijen et al.'s (2013) statistical route to describing trait variation is that it is well known that within a plant functional type at a site there is a large range of trait states, simply because species with differing trait values are more likely to coexist (Macarthur and Levins, 1967). Cody's (1986) delightful example of the divergent leaf traits of coexisting species of Proteaceae shrubs nicely illustrates this point. It follows that additional information and assumptions regarding limitations on the similarity of species need to be made when developing statistical models of community assembly (Laughlin and Laughlin, 2013). Future community assembly will be conditional on each localities community trait matrix and the community matrix is in turn defined, in part, by history. That is, while we recognise that a statistical approach may seem pragmatic, we suspect that it might be a dead end. By aggregating the effects of “different temporal and spatial scales, including acclimation, adaptation of species and species replacement” in statistical models (with a median R^2 value of 0.36) Verheijen et al. (2013) actually smooth away substantial components of the variation they themselves recognise as being essential for next generation DGVM models.

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We readily concede that the aDGVM2 as published in Scheiter et al. (2013) is a starting point, an illustration of the promise of one approach, a vehicle for encouraging a more intimate interaction between trait data and DGVM models. We are disappointed that Verheijen and colleagues felt it necessary to dismiss our contribution. To criticise a concept model because it is “not-validated” misses the point of a concept model. To criticise a published work for not “relating trait data to environmental variables” or for “not including trade-offs” when that work quite transparently does both is a questionable way to make progress in science. We hope that this comment has made some of the real differences between the two approaches more apparent to both developers and users of DGVM models. In summary the important difference is that Verheijen et al. (2013) use a direct statistical method to parameterise plant functional diversity, whereas Scheiter et al. (2013) define trade-offs between plant functional traits, which allows functional diversity to emerge as a by-product of the model’s dynamics.

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