

A deeper picture of biological communities

- ★ Many different factors affect the distribution of plants, insects and other species in the natural world, including not only their environmental requirements, but also their interactions with other species. The SESAM'ALP project aims to develop improved methods of modelling biological communities, as **Professor Antoine Guisan** explains

The dispersal, organisation and distribution of species in the natural world depends on many different factors. For a plant, temperature, light, water and nutrient availability are all important factors for example, now researchers in the SESAM'ALP project aim to develop improved models of plant and insect distribution, taking into account all the available information. "We try to incorporate all known influences on species distribution, and from that to reconstruct wider communities," says Professor Antoine Guisan, the project's Principal Investigator. This work builds on the SESAM (Spatially Explicit Species Assemblage Modelling ; see Fig. 1) framework, a community modelling scheme, effectively a series of modelling steps. "In the SESAM'ALP project we are aiming not only to test the SESAM framework, but to improve it," outlines Professor Guisan. "Over the past two years we've been working on these models for predicting the distribution of individual species, and from that moving to biological community predictions."

Environmental requirements

This starts from an understanding of a particular species' environmental requirements, what biologists call its environmental niche. While the environmental conditions are clearly important in terms of the development and survival of a species, Professor Guisan says there are also other factors to consider. "For example biotic interactions – interactions between species – will influence whether a species will be found in a given location, given the presence of other species. A specific location might be environmentally suitable for a species, but it might not be a very good competitor, and other species could exclude it," he explains. Another key factor to consider is the dispersal ability of a species. "Typically you find species within a specific distance from where they originated," says Professor Guisan. "These are the three main influences on species distribution, and they are all included in the SESAM framework."

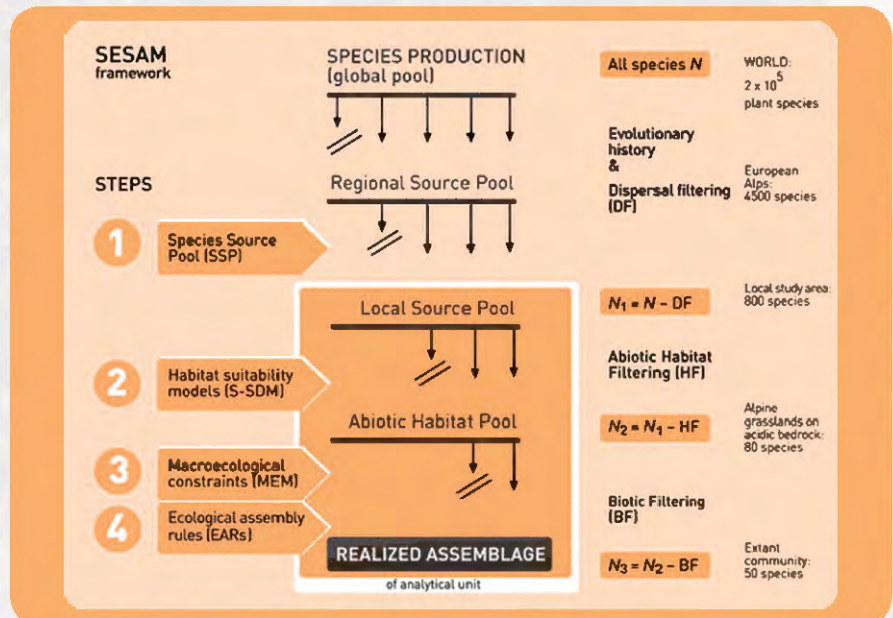


Fig 1: SESAM framework : Journal of Biogeography (2011) 38 / Guisan et Rahbek. © 2017 John Wiley & Sons, Inc.

A number of different methods have been proposed to build a deeper picture of ecological communities, among the most widely used of which is S-SDM (Stacked Species Distribution Models). Each species is modelled individually and a map of their distribution in a specific area is produced; scientists can then look to bring these maps together. "You can stack all the maps on each other, so that at the end you can

example if there is limited energy and nutrients at a site because you are in a cold climate system, then this might not allow as many species as in a tropical system. It may be that if there is low energy in a system there will be less species." This, however, is still a matter of debate (see below).

Nevertheless, stacking species distribution models can lead to overestimates of the number of species in a

Biotic interactions will influence whether a species will be found in a given location, given the presence of other species. A specific location might be environmentally suitable for a species, but it might not be a very good competitor, and other species could exclude it

accumulate species predictions for every site in a given area," explains Professor Guisan. This approach however ignores the biotic interactions, positive or negative, between species; Professor Guisan and his colleagues aim to integrate more information to reflect this complexity. "There might also be some further constraints on a given site, on the biological community," he says. "For

given site, so researchers are also looking to introduce top-down constraints (Fig. 2). "We can predict species richness in space using macroecological models (MEM), then use that to constrain the S-SDM prediction (Fig. 2 to 4). For example, your S-SDM prediction may predict 100 species in a site, and your macroecological model (MEM) predicts there would be 50," says Professor

Guisan. It might be the case that 50 species will not be able to survive in that specific site, so rules need to be identified to exclude those species. “These rules, the so-called ecological assembly rules, should be based on known interactions, like competition, predation, or other interactions that could lead to the removal of a species from a site for instance,” continues Professor Guisan.

The ecological assembly rules are an important dimension of the SESAM framework. The S-SDM is developed, which is then constrained with MEM, then on this basis researchers use assembly rules, such as the probability ranking rule (PPR; Fig. 3 and 4), to remove species that would not be in a real-life assemblage; Professor Guisan says that developing these rules is a major challenge. “It’s extremely difficult to quantify these rules,” he explains. While insights have been gained on some species from experiments, there is still much left to learn, so researchers have also been observing ecological communities in natural landscapes, such as the Swiss Alps. “We have been observing different communities, including different types of organisms and plants,” says Professor Guisan. “We are observing biological communities at a number of sites, and from this co-occurrence of species, we try to infer assembly rules. So from this we can say for example that across all the sites we have been surveying, two specific species always co-occur together, or never co-occur together.”

Biotic interactions

This latter case might be the result of a biological interaction, or it might just be because the two species do not occur in the same type of environment. Researchers aim to tease apart the different influences on species distribution and derive rigorous rules of biotic interactions from the available field data. “When species tend to co-occur, it might be that two species both like the same environment and are not in competition, or there could be facilitation between them, that one helps the other. Alternatively the opposite might be the case – two species may seem to have similar environmental requirements, but they very rarely co-occur together,” outlines Professor Guisan. This data will then be incorporated in the SESAM framework, using high-resolution environmental maps. “It’s almost a case of refining and improving the initial S-SDM map by adding these two further steps, the MEM and the assembly rules,” continues Professor Guisan. “We have been testing different approaches to these steps (Fig. 3 and 4).”

The species richness of a site is not the only major consideration in terms of constraining ecological communities and improving predictions, and researchers have investigated other possibilities. Along with considering the number of species at a site, Professor Guisan and his colleagues have also considered constraining predictions by functional – or trait – diversity. “For example think of a high-altitude site – tall trees or plants are less likely to survive there. So if you have both measurements of the height of species and predictions of the expected height for that type of environment, you will be able to exclude all species that are maybe too tall to survive there, as it’s too windy or cold,” he says. This approach was not as successful as species richness however in terms of improving the predictions. “We always

compare the predictions we make to independent observations. We build the model, we exclude the data that is not used to build the model, and we test the predictions on that independent data,” outlines Professor Guisan.

From these tests researchers learned that, unlike richness constraints, the inclusion of trait constraints did not generally improve the quality of predictions of ecological communities, and in some cases even had a negative impact. This might be due to the limited number of traits available, which mainly exist for above-ground characteristics (e.g. no trait measurements are currently available for roots), but it might also be partly caused by the difficulty of modelling the distribution of some individual species. “Typically, generalist species are more difficult to model than

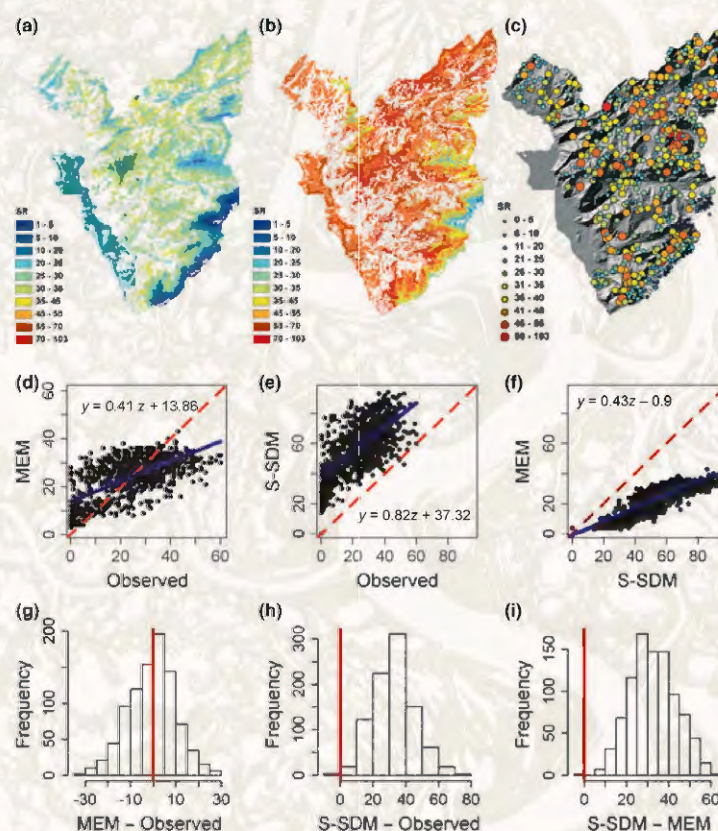


Figure 2. Predicted and observed plant species richness (SR) at 912 plots in open habitats in the western Swiss Alps (260 species) at a resolution of 25 × 25 m. (a) Estimated richness by macroecological modelling (MEM) using five variables – growing degree-days above 0 °C, moisture index, global solar radiation, slope and topographic position – and the average of four modelling techniques [generalized linear modelling (GLM), generalized additive modelling (GAM), gradient boosting model (GBM) and random forest (RF)]; see Dubuis et al. (in press). (b) Estimated richness by stacked species distribution modelling (S-SDM) using the same five variables and generating species distributions for each species using the average of the same four techniques used for MEMs. (c) Observed richness. (d) Scatterplot of MEM versus observed richness. (e) Scatterplot of S-SDM versus observed richness. (f) Scatterplot of MEM versus S-SDM richness. In scatterplots (d) to (f), the dotted red line represents the 1:1 relationship, and the plain blue line represents the regression line of a standard ordinary linear squares (OLS) regression across the cloud of points. (g) Histogram of MEM minus observed richness values. (h) Histogram of S-SDM minus observed richness values. (i) Histogram of S-SDM minus MEM richness values. In histograms (g) to (i), the vertical red line represents zero difference. Maps were generated and provided by Anne Dubuis (Dubuis et al., in press). / Guisan et Rahbek. © 2017 John Wiley & Sons, Inc.

specialist species. If a species has a very clearly defined ecology, it's easier to model than if it's present in a lot of places and we can't really identify the factors that drives it," explains Professor Guisan. There is still scope for further improvement, and alongside the work of his group in the Swiss Alps, Professor Guisan says the SESAM framework is also being tested elsewhere, testing its wider relevance. "The concept behind the framework is universal, in theory it could work everywhere," he outlines.

This is not to say that the theoretical foundations of the SESAM framework are beyond question though. The idea that there are constraints on communities, in terms of the number of species that can be supported in a specific community, is still a matter of intense debate. "Species richness as constraint is often discussed along with the idea of saturation. Is there a limit to the number of species that can coexist in a given community?" says Professor Guisan. Some scientists argue that there is no limit, as biological invasions tend to show that new species can always invade a community, but others take a different view. "Others say that there is saturation, that while a species could invade, over time the community will come back to its initial number, and maybe the invasive species

will replace a previously native species," continues Professor Guisan. "We recently published a paper in *Trends in Ecology & Evolution* about this question of how to deal with this saturation question in models."

The flexibility of the SESAM framework is an important attribute in this respect, as a constraint like the MEM can be added or removed as required. The wider goal in this research is improving the accuracy of predictions, which holds clear importance in terms of assessing the likely impact of climate and other environmental changes. "In SESAM'ALP we have been working to improve the models for individual species groups, and the SESAM framework," says Professor Guisan. "We are also working on the EcoGeoIntegrAlp project, in which we aim to improve plant distribution predictions by integrating further environmental data. For that, we are working on a multi-disciplinary basis, with environmentalists, geologists, hydrologists and others. We aim to predict two main ecosystem services – one is the aesthetic quality of the landscape, which is a very pressing question here in the Swiss Alps. The second is hydrological run-off. For example, if forests cover a larger surface area in future, how will this affect water flow down mountains to rivers, and thus water provision?"

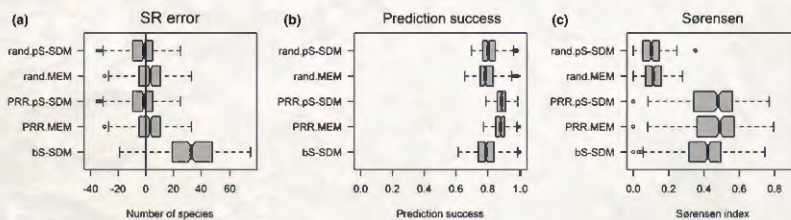


Figure 3. Boxplots comparing unconstrained stacked species distribution model (bs-SDM) predictions to results from the 'probability ranking' rule and random tests when applied constraining richness by the sum of probabilities from SDMs (PRR.pS-SDM and rand.pS-SDM, respectively) or by macroecological models (PRR.MEM and rand.MEM, respectively) (a, b, c). The metrics utilized in the comparison are: species richness error, i.e. predicted SR – observed SR (first column); prediction success, i.e. sum of correctly predicted presences and absences divided by the total species number (second column); and Sørensen index, i.e. a statistic used to compare the similarity of two samples (third column).

Journal of Biogeography (2015) 42 / D'Amen et al. © 2017 John Wiley & Sons, Inc.

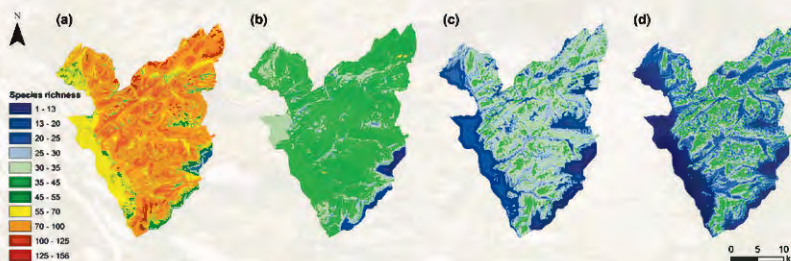


Figure 4. Predictions of species richness for the whole study area produced by (a) the unconstrained stacked species distribution model (bs-SDM), and by the application of the SESAM framework implemented with (b) the 'probability ranking' rule implemented with the sum of probabilities from SDMs (pS-SDM), (c) the 'probability ranking' rule implemented with the richness estimation by the macroecological model (MEM) and (d) the 'trait range' rule (using the combination of the three traits as constraints).

Journal of Biogeography (2015) 42 / D'Amen et al. © 2017 John Wiley & Sons, Inc.

At a glance

Full Project Title

Challenges in simulating alpine species assemblages under global change (SESAM'ALP)

Project Objectives

The knowledge gained at the end of the project, and the new innovative approaches, tools and datasets delivered, should foster important advances in our capacity of modeling and predicting communities across entire landscapes. In particular, it should allow addressing partially the question: will plant and insect communities evolve into novel assemblages under global changes?

Project Funding

Swiss National Science Foundation, SESAM'ALP project, grant nr 31003A-1528661, 480,000 euros.

Contact Details

Antoine Guisan, Full Professor
Head of the Spatial Ecology Group (ECOSPAT)
With affiliation to:
Dept. of Ecology and Evolution (DEE) &
Institute of Earth Surface Dynamics (IDYST)
University of Lausanne (UNIL)
1015 Lausanne, Switzerland
T: +41 692 42 54 / 36 15
E: antoine.guisan@unil.ch

Site of Spatial Ecology Group at the University of Lausanne (ECOSPAT) website:
W: <http://www.unil.ch/ecospat>

SESAM'ALP Project website:

W: <https://www.unil.ch/ecospat/en/home/menuinst/projects/main-projects/sesamalp.html>

EcoGeoIntegrAlp interdisciplinary project website:

W: <http://wp.unil.ch/integralp>



Professor Antoine Guisan

Antoine Guisan is Full Professor of Ecology at the University of Lausanne. His main focus is on spatial predictive modelling of plant and animal distributions, and the communities they form. His group is developing models for various applied purposes, such as rare species management, assessing climate change impacts and anticipating biological invasions.

Unil

UNIL | Université de Lausanne