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How do plant community ecologists consider the complementarity of observational, experimental and theoretical modelling approaches?

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ABSTRACT

Background and aims -- A large variety of methods are used by ecologists for studies at plant community level. While early works were mainly descriptive, more manipulative experiments are now being undertaken because they provide a better functional understanding and a greater insight into underlying mechanisms. Mathematical models are also being increasingly used, in particular for predicting biodiversity under global change. The aim of this study is to highlight the strengths, limitations, and advantages of these three approaches, namely observational, experimental and theoretical modelling.

Methods -- We assessed 149 papers published during the last four years in three specialized disciplinary journals (DJ) and 151 papers in three generalist high impact journals (HIJ) dealing with plant ecology, and checked the methods that were used. We asked participants of the ECOVEG7 meeting held in Switzerland (Lausanne, April 2011) whether observational, experimental and theoretical modelling approaches can, or should, be used alone or in combination when studying plant communities and ecosystem functioning in the context of global change.

Key results -- About 50% of articles published in both journal types used only a single approach. Nevertheless, papers in HIJ used the approaches in similar proportions, while articles in DJ had 8 times more observational than modelling studies. Combined approaches represented only 8% in DJ, while this percentage was more than double in HIJ.

Conclusion -- Plant community ecologists favour a combination of several approaches, but for practical difficulties (communicating among people using different approaches and publication strategies), single-approach studies are generally preferred. A combination of the three highlighted approaches seems to be the most appropriate way to respond to future challenges in plant community ecology such as biodiversity loss and impact of climate change as such studies require work on different temporal and spatial scales.

Key words -- Plant ecology, community ecology, approaches, observations, experiments, modelling, literature review.

INTRODUCTION

The field of plant community ecology or vegetation science has a long scientific tradition starting in the 19th century with A. von Humboldt, C. Darwin and E. Haeckel. It played an important role in the development of key concepts in biogeography and ecology (Deléage 1991). Since the beginning in plant ecology studies, descriptive and experimental approaches were combined to explain vegetation patterns and processes at various spatial and temporal scales. The notion of community itself was the object of a long debate between the Clementsian 'organismic' and the Gleasonian 'individualistic' concepts of plant communities (Clements 1916, Gleason 1926). The organismic concept has enabled the emergence and the development of phytosociology, often presented as a purely descriptive and qualitative approach of plant communities, although the ecological and functional aspects were already central to its founders (Braun-Blanquet 1964). The individualistic concept led to the development of quantitative tools to describe and explain gradients in species assemblages and diversity. Recently, these two conceptual views have been reconciled to explain the species assemblages in plant communities by a series of drivers and filters acting on the species pools at different spatial and temporal scales (Lortie et al. 2004).

Early studies in plant ecology were based on the observation of phenomena in nature. They were descriptive or comparative, including long-term observational studies in environmental monitoring. At the end of the 19th century, advances in plant ecology were often based on experimental laboratory studies or field experiments under controlled conditions (McIntosh 1986). One reason for this new approach was that observations made in new sites did not always conform to the expectations that were hypothesis from initial observations, thus preventing generalisation of the results. Moreover, experiments allowed disentangling factors at the origin of the observed responses, and could therefore give new insights in ecological interactions and underlying mechanisms. However, experiments on simplified communities in controlled conditions, as well as simple mechanistic models developed to explain their results, often led to paradoxes and controversies when confronted to observations in natural communities -- e.g. the paradox of the plankton (Hutchinson 1961), or the diversity-productivity debate (Hector et al. 2007, Loreau et al. 2001). With the increase of data acquired under diverse conditions and stored in databases (Kleyer et al. 2008), a theoretical approach has emerged in the 20th century (Coudun & Gégout 2006), based on statistical or mechanistic models which allowed understanding and predicting complex ecological patterns and interactions.

Today this panel of approaches is enlarged by the appropriation of molecular techniques to study the phylogenetic structure of plant communities in order to answer ecological and biogeographical questions (Parmentier & Hardy 2009, Webb 2000) or by barcoding for accurate species and community identifications (Kress et al. 2009). Furthermore, new concepts such as plant functional traits (Grime 1977, Lavorel & Garnier 2002) together with the advent of high capacity computers and multivariate statistical frameworks (Borcard et al. 2011, Leps & Smilauer 2003) are deeply modifying the field of plant community ecology and offer opportunities for cross-level studies (Gégout et al. 2005). For studies at a larger scale, remote sensing coupled to geographic information systems contribute to a worldwide assessment of vegetation communities and dynamics, facilitated by imagery allowing acquiring information for all habitats (Aragón & Oesterheld 2008), and in a short period of time compared to field-based surveys (Underwood et al. 2003, Xie et al. 2008). Meta-analysis is another tool allowing integration of information acquired independently in various sites and extracting general patterns (Dormann & Woodin 2002, van Kleunen et al. 2010).

The complementarity of these approaches is highlighted in most standard books on methods in ecology (see for example Henderson 2003). While most authors emphasise that experiments cannot be done effectively without knowing the natural history of the studied organism, community or ecosystem, or the environmental background, many studies are undertaken without thorough preliminary survey and observation of the studied phenomena in nature. In many cases, challenges such as time limitation or shortage in funds are put forward to justify this partial approach. However, we argue that such arguments are blinkered: a preliminary study may save both money and time in the long run because it reduces the risk of an inadequate sampling effort or pitfalls in the experimental set-up. Similarly, modellers may reach more rapidly a representative mathematical model if they have already observed the phenomena in nature. Obviously, communication among colleagues with different approaches (i.e. observers, experimentalists, modellers) may help to improve the knowledge of ecological systems.

This paper reviews the approaches used in recently published works in plant community ecology and summarises the outcome of a plenary discussion devoted to this topic at the ECOVEG7 international meeting held in Switzerland (Lausanne, April 2011) which brought together ecologists from mainly French speaking countries. We aimed at characterizing the approaches currently used in this field and identifying options for their use. We addressed the following questions more specifically: i) what are the specificity, strength, and limitations of each of the three approaches (observations, experiments, models)?; ii) are these approaches exclusive or should they be combined in the study of ecological processes?; and iii) what are the challenges in combining these approaches? We hypothesised that high impact journals publish more papers in which combined approaches were used, as their scope is more generalist than in specialised disciplinary journals, which mainly focus on single-approach papers.

MATERIAL AND METHODS

For assessing the methodological approaches used in published works, we compared two groups of journals formed by three generalist high impact journals (*Nature*, *Proceedings of the National Academy of Sciences*, *Science*; thereafter "HIJ" journals) and by three disciplinary journals (thereafter "DJ" journals) dealing specifically with plant ecology (*Perspectives in Plant Ecology and Evolution*; *Plant Ecology and Evolution*; *Plant Ecology & Diversity*). Among the high number of disciplinary journals, these three journals were chosen as their number of articles published during the selected period was similar to those of the HIJ (cf. results). We therefore deliberately did not select journals such as *Applied Vegetation Science* (190 published articles during the selected period), *Journal of Vegetation Science* (353) or *Plant Ecology* (641). The search was performed via the Web of Knowledge (accessed on 19 May 2011) with the search string "Publication Name=(Plant Ecology & Diversity OR Perspectives in Plant Ecology and Evolution OR Plant Ecology and Evolution)" and the key word "plant ecology" in either title or keywords. We restricted the search to the document type "article" and the time span 2008--2011, as we were interested in recent trends. A similar search with changed publication name was done for the HIJ. We assessed whether the results presented in the paper were observational (OBS), experimental (EXP), obtained from a model (MOD), or any kind of combination of the three approaches. This was done by reading the abstract, or when the information was not clear from the abstract, by checking the entire paper. Papers primarily focusing on taxonomy, genetics, or literature study were not considered.

During the plenary session at ECOVEG7, a discussion was launched on this topic, animated by a moderator. The first part of the discussion concerned the specificity, strength, and limitations of each of the three approaches, the second part was on the usefulness of either single or complementary approaches, and the third part concerned the challenges of combining methods. The following questions were submitted to the participants by mail one week before the conference:

- What are the criteria allowing you to select or use a particular approach to answer a scientific question in relation to ecosystem functioning in the context of global change? What would be your preferred approach in plant community ecology?
- Would one approach be sufficient to answer your scientific questions? Would it have been more efficient to combine several approaches (e.g., modelling based on monitoring data)?
- Are modelling and short-term observations compatible and complementary when studying ecosystem functioning in a context of global change?
- Under what circumstances is a particular approach best adapted and effective? Is one of these approaches suitable for any situation?

Replies were sent by return mail and collected by the organisers of the conference.

For identifying what the authors of scientific articles in ecology and plant ecology propose as methodological outlook, we checked the number of references in Google Scholar (accessed 21 Jun. 2011 and 11 Jul. 2011) that contained “ecology” or “plant ecology” together with 11 formulations calling for either more observations, monitoring, experiments, empirical studies or modelling. We assessed the trends for these search terms based on the number of hits obtain in Google Scholar (table 1).

RESULTS & DISCUSSION

Current approaches used in published studies

Web of Knowledge revealed 186 papers published in the last four years with the keyword “plant ecology” in the three investigated HIJ journals and 156 papers in the three investigated DJ journals. After a first screening we excluded 35 papers from HIJ journals as the subject of the paper did not concern plant ecology, and 7 papers from DJ journals as they were double entries in the database. This resulted in 300 papers (for the complete list of all papers see app. 1), 151 HIJ-papers and 149 DJ-papers on which the following analysis is based.

Out of these 300 papers, 31% HIJ-papers and 42% DJ-papers dealt with non-ecological subjects (taxonomy, genetics, GIS, etc.). From the remaining, 49% of HIJ-papers and 50% of DJ-papers used only a single approach, but the partitioning between the three approaches differed (fig. 1): while papers published in HIJ journals used a similar proportion of each approach, about 8 times more observational studies were published in DJ journals as compared to studies using modelling approaches. Combined approaches represented the minority in DJ journals, with only 8% of the published papers, while this percentage was more than double in HIJ journals.

These results were obtained from journals which we deliberately selected as being not limited to one approach. However, a tendency towards publishing in specialised journals can be observed recently. Approach-based journals such as "Ecological Modelling", "Environmental Modelling & Software" or "Environmental Modelling & Assessment" have been launched in the mid-1970s and focus mainly on a single approach (e.g. modelling). Studies dealing with models in plant community ecology are published in these specific journals and have been neglected in our analysis. However, articles concerning observational data may also be published in specific journal such as "Journal of Environmental Monitoring" or "Environmental Monitoring and Assessment" and therefore similarly omitted from the present analysis.

Observations, Experiments, Models -- Specificities, strengths, and limitations

The participants of ECOVEG7 agreed that observational or descriptive studies constitute a strong basis for further investigations since they reveal natural patterns and therefore the field reality to be studied. Observational data are also necessary for long term environmental studies such as vegetation monitoring. However, acquiring new vegetation relevés is time-consuming, expensive, and the results are often not publishable. As one of the participants summed up: "Who is doing the vegetation relevés we'll use in 50 years?". Many advances have been made in recent years to bring together the numerous vegetation data collected by different institutions and people. However, these data are still dispersed in several databases such as, in France, SOPHY (http://sophy.u-3mrs.fr/sophy.htm), EcoPlant (https://www2.nancy.inra.fr/unites/lerfob/ecologie-forestiere/bd/ecoplant.htm), Phytobase (http://www.tela-botanica.org/page:liste_projets?id_projet=18&act=documents&id_repertoire=16428), e-Flora-sys (http://eflorasys.inpl-nancy.fr/) and FlorEM (Spiegelberger et al. 2010). Recently some attempts were undertaken to create a global database (Dengler et al. 2011, Kattge et al. 2011) overcoming geographical limitation. Nevertheless, both regional and global databases are confronted to similar problems such as the ownership of the data (Janßen et al. 2011), their accuracy, and the missing coverage in certain regions and for certain periods (Dengler, et al. 2011).

According to the participants, the main drawbacks of experiments in ecology are their limitation in time and space (Jenkins & Ricklefs 2011) and the difficulty to use their results beyond the targeted question. As a matter of fact, young researchers at both MSc and PhD levels often prefer short term experiments since this approach has a higher potential for results obtained factors, reducing considerably the chances of a good comprehension of the system. This impedes integration of experimental results in a wider context. To overcome such limitations, several possibilities were mentioned during the discussion. Multi-site experiments with a standardised protocol were cited as the best solution to investigate and validate processes at large spatial scales (e. g. Bernhardt-Romermann et al. 2011). If experiments were designed independently and a joint data analysis was not planned beforehand, meta-analysis could be a powerful tool to surmount such limitations (Osenberg et al. 1999). Nevertheless, this requires the awareness of the existence of similar experiments and the network to join efforts. The online database PermanentPlots.CH (http://www.unil.ch/ecospat/page48113.html), which stores historical data about permanent plots in Switzerland was mentioned as an example of an integrating research initiative.

Model calibration and validation require sound data originating from both observational and experimental studies. It is therefore an important prerequisite, as mentioned during the discussion, that the data are adapted to the model. For example, fine-scale observations are not appropriate for predictions at broad scale, and experiments focusing only on one or two factors rarely represent the complex interactions that operate in real systems that a model wants to reproduce.

Methodological choices -- science-driven or fashion-driven?

Interestingly, the percentage of experimental studies has changed during the last 5 decades: in 1959 (Hairston 1989), experimental studies represented only about 4 % of the articles published in both *Journal of Animal Ecology* and *Ecology* and 16% in *Journal of Ecology*, but this percentage increased to about 33% in 1987 for the first two journals, and 26% for the latter. In our literature study, this percentage was about 15% for both, disciplinary and high impact journals. Such trend to more experimental studies has also been observed by the participants of ECOVEG7 and was explained by the opportunistic behaviour of researchers who choose the approach that allows them to increase the probability of being rapidly published. While everybody agrees that the choice of an approach should be science-driven, the pressure to publish apparently overwhelms this.

From a scientific perspective, all three approaches have their limitations and advantages, as raised by the participants of ECOVEG7. The choice of the appropriate approach is however a trade-off between the initial scientific question (patterns, processes, predictions; applied vs. theoretical ecology), personal or institutional skills, and publication strategy. Personal limitations, as most researchers do not possess the knowledge necessary to apply all methods, but also infrastructure, budget, institutional structure and science-policy, guide in many cases the decision in favour of one approach over another. In addition, as mentioned repeatedly, fashion is also governing science (Belovsky et al. 2004). Trends such as the increase of models and the decrease in observational studies published in the last years may represent such fashions. However, the scope of journals or subjective preferences of editors or reviewers may contribute equally to the high number of publications using models in HIJ journals, and to their low percentage in DJ (fig. 1).

Experimental results often fail to explain properly the patterns and processes being studied, which is at least partly due to the diverse methodological approaches and lack of concerted protocols based on sound observation and coordination between scientists. The difficulty of correct interpretation of observed patterns by means of experimental evidence has been raised many times. Science historian H. Cravens stated that in the early 20th century experimentalists overshadowed people doing observations or descriptive work, and that the context or nature in which the experiment was done did not get enough consideration (Cravens 1978). The steadily increasing body of literature based on experiments is one evidence of the trend (Jenkins & Ricklefs 2011). Today, this trend seems to be reversed, as observational approaches are greatly enhanced by technological advances in remote sensing, microscopy, genetics, animal-borne sensors, and computing which make basic observational approaches in ecology far more powerful than at any point in scientific history (Sagarin & Pauchard 2010).

Combining approaches -- difficult, but promising

Participants of ECOVEG7 agreed that for a more complete study of ecosystems, approaches should be combined. However, our literature study revealed only three papers published in HIJ journals (Brando et al. 2010, Desurmont et al. 2011, Roper et al. 2010) in which all three approaches were combined

As requested for ecology in general, vegetation studies should be more integrative and incorporate observational approaches in experimental studies and experimental approaches in modelling (Belovsky, et al. 2004). As a consequence, studies would become more comprehensive if experiments were based on patterns observed in nature, then hypotheses clearly formulated and tested individually with experiments. However, too often “hypotheses are generated by « vote » within teams or dictated by the funding agency, which make no sense scientifically” (Likens 1998, p.255). Results obtained from observations and experiments should be used to build models allowing a more mechanistic understanding of the ecosystem and predictions about its future development. While it would be wishful to see more researchers who possess a background in all three approaches, participants emphasised the fact that institutions, such as universities and research institutes, may be the best place where people with different methodological background could be associated. Affiliations of researchers using different approaches will promote integrated research spanning from the observation of phenomena in nature over experiments to prediction by models.

Several of the participants underlined the need for combining the three approaches for a better understanding of ecosystem processes and functioning and the response of plant populations and communities to global change. This motion is in accordance with recent ideas on combining observations and experiments in the study of global change, as both are strengthened when reconciled (Sagarin & Pauchard 2010). The ideal way to study plant communities and interactions is to observe patterns in nature, which allows for the formulation of hypotheses that are focused on a number of factors of potentially high importance as drivers of the patterns observed. These factors should be prioritised according to the patterns observed, but also with respect to future modelling and therefore be elaborated in partnership among the modeller, the experimentalist and the observer. Depending on the outcome of a first modelling step, the experimentalists and the observers should continue to acquire field data or do further experiments, but with a more focused perspective. With this iterative process, a more realistic or general model can evolve and experiments or observations will in turn be more specific. The methodological triad (fig. 2) conceptualises the complementarity of the three approaches and shows their interplay. Hypotheses can either be formulated based on observations in the field or - if already existing - on models. These hypotheses can then be tested with empirical explanatory models, either directly by manipulative experiments or indirectly by targeted observations along environmental gradients. In the first case it yields a predictive model based on explicit causality, in the second it yields a forecasting static model with implicit causality. The hypotheses can also be verified by means of theoretical models that are based on given reciprocal interactions and yield predictive dynamical models based on causal processes. However, confirming hypotheses derived from observations may lead to vicious circles if hypothesis creation and their testing are based on the same data. It is therefore crucial to resample an independent data set. Similarly, the theoretical models need to be validated with an additional data set.

It is obvious that this iterative approach is time consuming and expensive, and can only be rarely achieved in a single project, considering their average duration of one to three years, or by a single person. A proposition that emerged at ECOVEG7 was that research institutions should pay more attention to the complementarity of scientist’s background, so that groups with large and various expertise could be built. Interdisciplinary approaches should be favoured (Likens 1998), even though the communication between different scientific communities could be difficult (Miller et al. 2008). It would also be necessary that such groups can work on a common topic for several years. Other ways to overcome an individual researcher’s incomplete expertise and to excel in several approaches is to bring people together to tackle a common project, as it is done, for example, in the long-term ecological research (LTER) sites (Likens 1998). Such an approach was recently promoted with the establishment of the Central French Alps long-term socio-ecological research platform (LTSER Central French Alps, Lavorel et al. 2012). Based on earlier observational studies, a common project was developed which brought together researchers from different disciplines, but also those who used different approaches. This paves the way for more in-depth study of ecological questions. The advantage of such research structures would be manifold and would trigger breakthrough research in deepening the functional approach and also result in increasing individual competences. Such groups have a high potential for outputs publishable in HIJ journals, as demonstrated by our literature review.

Nevertheless, even if there was general agreement at ECOVEG7 that the approaches are complementary, it is often difficult to promote such integrative projects. For instance, scientists are evaluated on the basis of published articles, and in many cases it is thought to be easier and more productive to conduct small experiments, rather than trying to have a more complete view requiring several approaches and surely more time. Moreover, a common problem encountered during collaborative, interdisciplinary projects that combine experiments and models, is that people performing the experiment and researchers elaborating the model do not use the same technical language, and often do not have the same objectives (Miller, et al. 2008). As a consequence, a huge experimental effort is sometimes accomplished, but only a conceptual model is developed, or the results obtained by experiments cannot be used properly to validate the model.

Today's observations -- tomorrow's bases for experiments and models

Our investigation concerning the future directions of research reveals a similar demand from both authors of published articles and participants of ECOVEG7. In total, the combination of the search terms revealed 2,466 hits in Google Scholar with the broader term "ecology" and 117 when restricted to "plant ecology" (tab. 1). In most cases, authors propose to continue or underpin their study with more long-term observations (50% in ecology and 56% in plant ecology) or with further experiments (38% in ecology and 25% in plant ecology), while none of the papers argued for more models in plant ecology. Similarly, the contributors to the plenary discussion at ECOVEG7 expressed concern about the difficulty of collecting field data. However, some of the currently highly cited papers in ecology are based on the exploitation of large databases (Lenoir et al. 2008, Thuiller et al. 2005), which were fed by vegetation relevés done in earlier years when field observation was more fashionable. Today, such data are mainly collected by organisations in charge of inventories and biodiversity surveys, such as national botanical conservatories and national/regional parks. This is a valuable step, but the objectives of the above-mentioned institutions might not be the same as for plant community ecologists concerned with ecosystem functioning and their response to global change. As a consequence, the collected data may neither meet the requirements for topical research questions, nor for sound statistical analyses. Collaboration between conservatories and national/regional parks on one hand, and universities or research institutes on the other hand may help to optimize the invested time and money. Beforehand, cooperation during the design of monitoring programs would probably increase the added value of such databases. In particular, the task of conservatories and parks for acquiring information on the current vegetation could be efficiently linked to scientific goals such as future analysis of impact of land-use or climate changes on plant communities. As an important side effect, some difficulties in relation to the data ownership may be avoided.

Expert knowledge & financial funding-- sufficiently available and well distributed

Acquiring sound data from observational studies is a main issue in general, but in particular in the current context of global change, where simulations are needed to guide public decision (Sutherland 2006). The experience to accurately conduct field observation, i.e. the expertise to correctly identify species and to describe a plant community, needs to be recognised as an important scientific aspect for high quality data and their subsequent potential use. Otherwise, and this can already be observed today, young scientists are discouraged to specialize in taxonomy or plant community description (Pearson et al. 2011). Moreover, human resources are unevenly distributed with a high number of taxonomists in well-developed countries, while less developed countries, which harbours comparatively a higher number of species, have only limited expert knowledge (Gaston & May 1992). A further aspect concerns easy access to software and computers, or - more generally - to financial support needed to use experimental or modelling approaches. Most of the plant biodiversity is located in developing tropical countries where good quality descriptive information is essential for biodiversity conservation programs (Ahrends et al. 2011).

CONCLUSION

We found that plant community ecologists mainly publish descriptive and experimental studies in disciplinary journals, a conclusion which was also made by the plant community ecologists attending ECOVEG7. They favoured a more comprehensive approach, but practical difficulties (e.g. to communicate between people using different methods) and an increasing need for specialization drive them to carry out single-method studies, despite the fact that multi-method studies allow to assess ecological processes in a more complex way and have a higher potential for being published in generalist high impact journals. The importance of using combined approaches will probably increase in the future because studies on key issues in the context of global changes, such as biodiversity loss and impact of climate change, require approaches that can be used at different temporal and spatial scales. A combination of the three highlighted approaches seems to be the most appropriate to respond to these challenges in plant community ecology.

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Figure captions

Table 1 -- Combined search on Google Scholar with two search terms. Accessed 21 June 2011 and 11 July 2011.

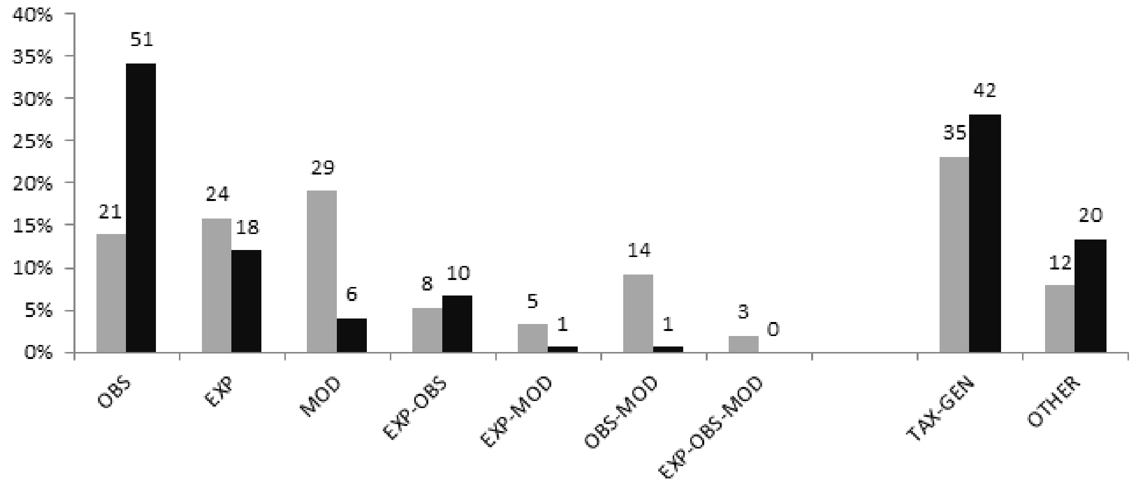
Figure 1 -- Percentages and absolute numbers of papers dealing with plant ecology using different approaches. The sample was restricted to articles published between 2008 and mid 2011. Grey bars: High Impact Journals (Nature, PNAS, Science); black bars: disciplinary journals (Plant Ecol Divers, Perspec Plant Ecol, Plant Ecol Evo). OBS, observation; EXP, experiment; MOD, modelling; EXP-OBS, EXP-MOD, OBS-MOD, EXP-OBS-MOD, combination of different approaches; TAX-GEN, taxonomic and genetic approaches; OTHER, other approaches like literature studies, cost-benefits analysis, etc.

Figure 2 -- The methodological triad and its application to plant community ecology.

TABLE 1

Table 1 -- Combined search on Google Scholar with two search terms. Accessed 21 June 2011 and 11 July 2011.

Search term	"plant ecology"		"ecology"	
	Hits	%	Hits	%
"more observational studies are needed"	0	0,0%	3	0,1%
"more observations are needed"	8	6,8%	203	8,2%
"new observations are needed"	0	0,0%	6	0,2%
"further observations are needed"	5	4,3%	179	7,3%
"more monitoring is needed"	1	0,9%	30	1,2%
"monitoring is needed"	57	48,7%	1350	54,7%
"more experimental studies are needed"	13	11,1%	62	2,5%
"more experiments are needed"	24	20,5%	436	17,7%
"more empirical studies are needed"	7	6,0%	117	4,7%
"more models are needed"	0	0,0%	12	0,5%
"new models are needed"	2	1,7%	68	2,8%
Total hits	117	100%	2466	100%



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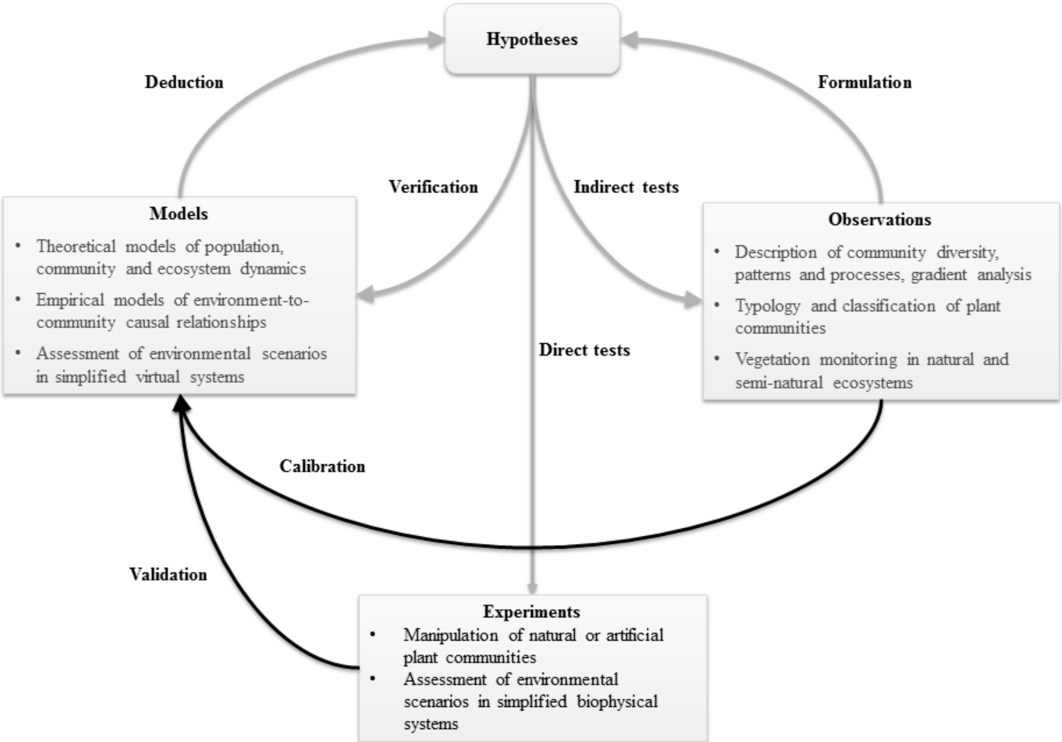

Figure 2 -- The methodological triad and its application to plant community ecology.