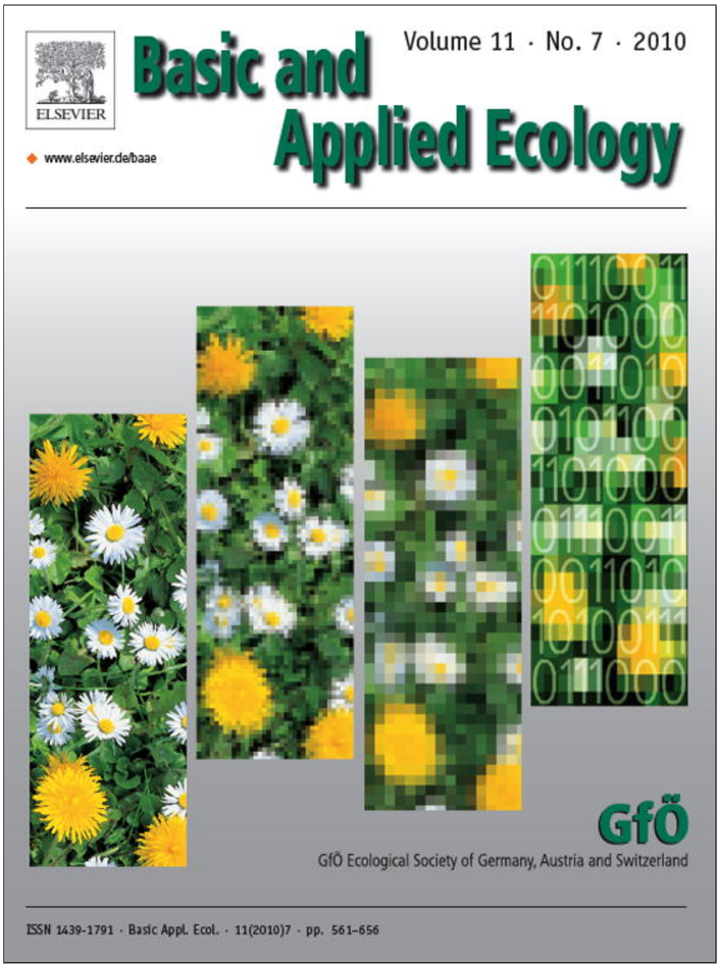
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Predicting population and community dynamics: The type of aggregation matters☆

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Abstract

When investigating complex ecological dynamics at the population or community level, we necessarily need to abstract and aggregate ecological information. The way in which information is aggregated may be crucial for the outcome of the study. In this paper, we suggest that in addition to the traditional spatial, temporal and organizational levels, we need a more flexible framework linking ecological processes, study objects and types of aggregation. We develop such a framework and exemplify the most commonly used types of aggregation and their potential influence on identifiable drivers of community dynamics. We also illustrate strategies to narrow down the range of possible aggregation types for a particular study. With this approach, we hope (i) to clarify the function of aggregation types as related to traditional ecological levels and (ii) to raise the awareness of how important a deliberate way of aggregating ecological information is for a sound and reliable outcome of any empirical or theoretical ecological study.

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Zusammenfassung

Um komplexe ökologische Dynamiken auf der Ebene von Populationen oder Lebensgemeinschaften untersuchen zu können, müssen wir ökologische Informationen abstrahieren und aggregieren. Die Art und Weise, in der wir die Information aggregieren, kann bestimmend für die Untersuchungsergebnisse sein. In diesem Artikel schlagen wir vor, dass zusätzlich zu den traditionellen Skalenebenen, die sich auf Raum, Zeit und Organisation beziehen, ein flexibleres System benötigt wird, das ökologische Prozesse, Studienobjekte und Aggregationstypen in Beziehung zueinander setzt. Wir entwickeln ein solches System und erläutern exemplarisch die häufigsten Aggregationstypen und ihren potenziellen Effekt auf zentrale Einflussfaktoren der Dynamik von Lebensgemeinschaften. Auch zeigen wir Strategien auf, mit denen die Bandbreite möglicher Aggregationstypen für eine Untersuchung eingegrenzt werden kann. Wir hoffen, dass wir mit diesem Ansatz (i) die Funktion von Aggregationstypen im Vergleich zu den traditionellen ökologischen Skalenebenen verdeutlichen können und (ii) dafür sensibilisieren können, wie wichtig ein bewusster Umgang mit der Aggregation ökologischer Information für die Stichhaltigkeit und Zuverlässigkeit der Ergebnisse jeder empirischen und theoretischen ökologischen Untersuchungen ist.

Keywords: Scales; Organizational level; Pattern–process relationship; Trophic guild; Functional type; Species; Phenotype; Genotype; Body size class; Study design

Introduction

A major aim of ecological research is to understand and predict spatio-temporal patterns of population and community dynamics, such as the geographic distribution of plant and animal species and the stability of communities. Such patterns represent highly aggregated information whose explanation may sometimes require only basic ecological processes and little detail. For example, the productivity of a grassland may just be explained by aggregated information such as the diversity of the community (Tilman et al. 2001). However, population- and community-level patterns typically arise from processes that can only be captured by considering much greater levels of ecological detail. For example, explaining grassland productivity may not only require information on community diversity, but also depend on the abundance of functional types, such as legumes. Disaggregating further, we may find that some legume species rely more on symbiotic nitrogen fixation than others do and that suitable species combinations between legumes and rhizobia are crucial for the functioning of the symbiosis (Sprent & Sprent 1990). Finally, the amount of fixed nitrogen can vary depending on specific combinations of genotypes of both legumes and rhizobia (Bourion et al. 2007) and genotypic traits of legumes can importantly affect interactions with further associated organisms (Kempel, Brandl, & Schädler 2009). The crucial task for the researcher is to decide how much aggregation is possible given the desired spatio-temporal resolution of the phenomena to be explained.

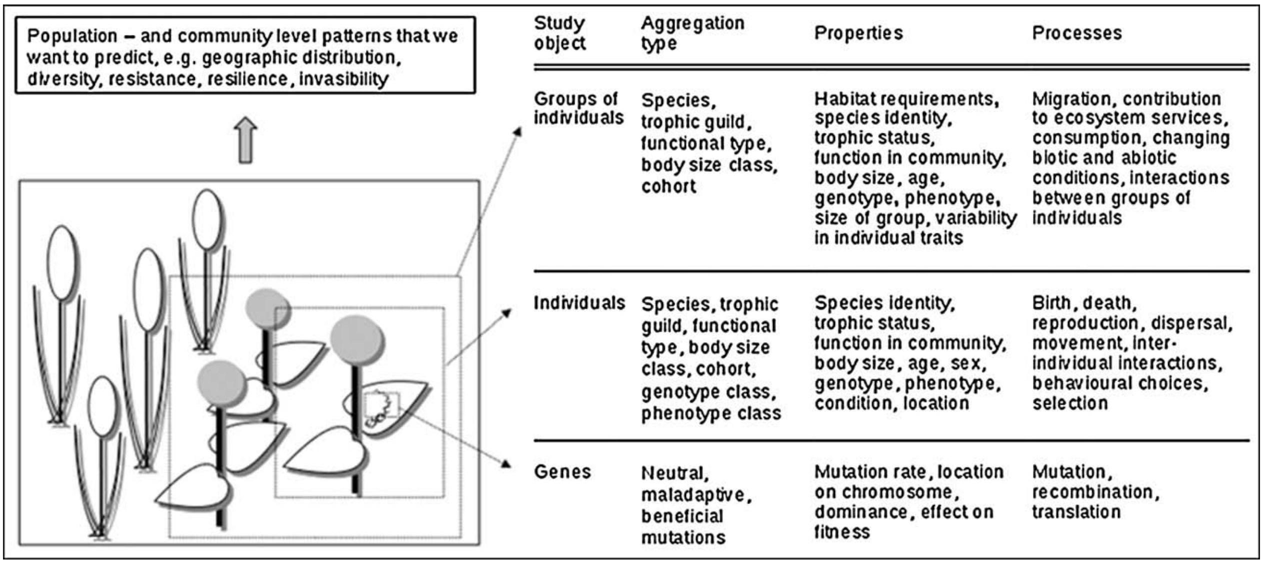
The grassland productivity example suggests that the decision to focus on functional types, species or genotypes can qualitatively alter the outcome of a study. Observed differences in ecosystem productivity may be explained by functional type identity, species identity or even genotype differences. However, there is no rigorous methodological approach or general rule for identifying the degree of aggregation providing an optimal balance between the remaining uncertainty in the results and the invested effort.

Clearly, the topic of how to choose an optimal degree of aggregation is too complex and general to be fully treated in a single paper: first, the optimum degree of aggregation strongly depends on the specific question asked in a study; second, our ecological knowledge on the processes affecting population- and community-level dynamics is far from being complete. Nonetheless, in each study, we explicitly or implicitly base our analysis on a particular degree of aggregation. Therefore, the aim of this paper is to give an overview of aggregation categories in ecology, organize them into a classification framework and synthesize current knowledge on how to approach the choice of the type of aggregation during the design of ecological studies. These considerations, we hope, will help to increase the awareness of the importance of aggregation types in ecological research.

In the following, we will first present a classification framework that reflects the relationships between study objects (e.g. groups of individuals), their properties (e.g. trophic preferences) and associated aggregation types (e.g. trophic guild), and ecological processes (e.g. food consumption). Second, for a few aggregation types commonly used in ecological research, we exemplify how the decision for a particular type of aggregation can influence the outcome of a study. Finally, we develop first strategies for approaching the question of how to choose an aggregation type for a particular investigation of population and community dynamics.

A classification framework

In ecology, the aggregation of ecological information has traditionally been described with three types of characteristics (*sensu* Levin 1992): the spatial scale, the temporal scale and the hierarchical levels of organization, i.e. individuals, populations and communities (see also Reuter et al. 2010).



Study object	Aggregation type	Properties	Processes
Groups of individuals	Species, trophic guild, functional type, body size class, cohort	Habitat requirements, species identity, trophic status, function in community, body size, age, genotype, phenotype, size of group, variability in individual traits	Migration, contribution to ecosystem services, consumption, changing biotic and abiotic conditions, interactions between groups of individuals
Individuals	Species, trophic guild, functional type, body size class, cohort, genotype class, phenotype class	Species identity, trophic status, function in community, body size, age, sex, genotype, phenotype, condition, location	Birth, death, reproduction, dispersal, movement, inter-individual interactions, behavioural choices, selection
Genes	Neutral, maladaptive, beneficial mutations	Mutation rate, location on chromosome, dominance, effect on fitness	Mutation, recombination, translation

Fig. 1. A classification framework defining aggregation types commonly used when predicting population- and community-level patterns in relation to categories of study objects, their properties and ecological processes. The framework can be applied to plant (illustrated on the left), animal or mixed communities.

In parallel, the classification into further categories, such as functional types, trophic guilds, body size classes, genotypes, and phenotypes has become common practice, adding a new facet to the concept of aggregation and thus complicating the choice of an adequate degree of aggregation. In the first instance, the development of additional classification types was motivated by the insight that population and community dynamics can often be better understood and predicted when abandoning the traditional focus on species. However, a general framework for the new aggregation types is lacking so far. In the following, we propose a concept for such a framework by breaking down organizational levels into study objects on the one hand and types of aggregation on the other hand.

With the term *study object* we refer to the investigated agents of a study, such as genes, individuals or groups of individuals (Fig. 1). Derived from scientific practice, this is a basic operational definition requiring as little structural or functional information as possible: The study object carries an identity (e.g. ‘individual 17’). This identity, however, does not provide any ecological information. Study objects are the smallest units we can focus on in a study. For example, if the study object is a group of individuals, there is no point in differentiating between single individuals in the group. In an empirical approach, the study objects are the units on which we collect data: if we record the height of single plants, the study objects would be individuals; if we measure the area covered by a population, the study object would be a group of individuals. In an agent-based modelling approach (cf. Grimm & Railsback 2005), the study objects are typically represented by the agents of the model.

Study objects can be characterized by their *properties*, such as species affiliation or body size (Fig. 1). Those properties that are regarded as relevant for the study question should be used as aggregation criteria. If used as an aggregation criterion, each property is linked to an *aggregation type*, e.g. ‘function in the community’ is linked with ‘functional type’. Information about the study objects that is not captured by the selected properties and thus by the aggregation type is ignored, resulting in the aggregation process.

The aggregation types that we define here differ from levels of spatial and temporal aggregation, because they do not necessarily have to follow a hierarchical structure. They can be nested as in the case of species and genotypes, where a genotype is always associated with exactly one species identity (Fig. 2). However, most of the aggregation types do not form clear hierarchical levels of aggregation, hence the designation ‘aggregation *type*’ as opposed to ‘aggregation *level*’. For instance, the body size of an individual is often cor-

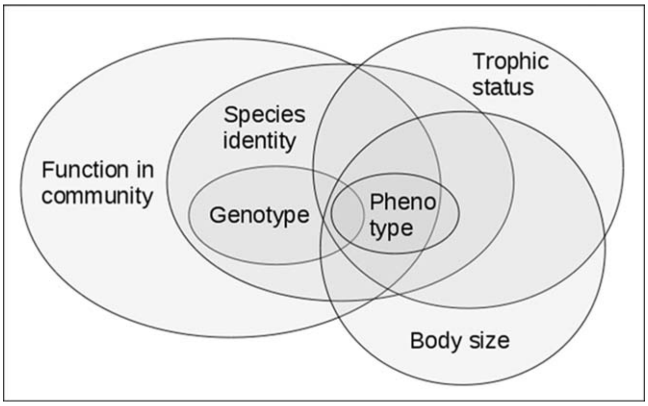


Fig. 2. Different types of aggregation can be nested such as phenotypes in species, body size and trophic status or may have no unique hierarchical structure such as in most other cases.

related with its trophic status (large overlap in Fig. 2), but the correlation is not perfect. Similarly, species identity may not be a good predictor of body size class or trophic guild, because body sizes and trophic preferences may depend on age, life-stage, individual or population history, as well as on environmental conditions.

Different ecological *processes* are relevant for different study objects and aggregation types, covering a great range of spatial and temporal scales (Fig. 1; see also Reuter et al., 2010). The chosen aggregation type determines the processes that can be investigated. Processes at greater levels of aggregation than the chosen one can be addressed by scaling-up procedures such as agent-based modelling (e.g. Meyer, Wiegand, Ward, & Moustakas 2007) or moment approximations (e.g. Calabrese, Vazquez, López, San Miguel, & Grimm 2010; see Reuter et al., 2010 for a more comprehensive treatment of scaling-up approaches).

Applying types of aggregation

In the following paragraphs, we characterize a few of the types of aggregation more commonly used in ecology, evaluate advantages and disadvantages when using them for predictions of community-level patterns, and present example applications. Some of the examples highlight the strong effects a decision on a particular type of aggregation can have for the outcome of a study.

Genotypes

Genetic diversity is a basal component of biodiversity. The genetic composition of populations influences the ability of species to persist under environmental change, to interact with other species and consequently to maintain the structure and dynamics of communities (Hughes, Inouye, Johnson, Underwood, & Vellend 2008). Evolutionary responses to environmental change are predicated on selection pressures that act on intraspecific genetic variability (Hoffmann & Willi 2008). Such responses are reflected in changes of the genetic make-up of populations on ecologically relevant time scales with consequences for communities and ecosystem processes (Hughes et al. 2008). There are numerous examples of effects of genetic composition and diversity on populations, communities (both within and across trophic levels) and ecosystems (reviewed in Hughes et al. 2008). For instance, a growing body of literature demonstrates bottom-up effects of plant genotype on the performance and community structure of associated consumers (e.g. Underwood & Rausher 2000; Johnson 2008) and genotype-by-genotype interactions involving plants and insects (e.g. Tetard-Jones, Kertesz, Gallois, & Preziosi 2007). These effects have also been shown to extend to key organisms of ecosystem processes like soil microflora (Schweitzer et al. 2008) and decomposers (e.g. Madritch & Hunter 2005) and may also create spatial mosaics of genetically mediated ecosystem processes (Madritch, Greene, & Lindroth 2009). However, genotypic influences are most likely to have important community- or ecosystem-level consequences if occurring in dominant and foundation species (Whitham et al. 2006). The consideration of genotypes is essential in studies where evolutionary changes and genetic differentiations may provide explanatory value for the investigated processes (e.g. invasions). Studies at the genotype level are further suitable for any situation where there is genotypic variation in ecologically important traits, especially if the resulting phenotypic variation within species equals or exceeds that among species (see Bangert et al. 2005; Shuster, Lonsdorf, Wimp, Baily, & Whitham 2006; Schweitzer et al. 2008 for examples). However, using the level of genotype for ecological studies is often hampered by the unavailability of information on the genetic identity of individuals.

Phenotypes

Some organisms exhibit large degrees of phenotypic plasticity, e.g. in morphology, life-history traits or behaviour. This plasticity can buffer the effects of biotic interactions, such as competition or predation, and ultimately affect community structure. In these cases, a study should distinguish between different phenotypes, instead of aggregating to species identity. For example, fennel pondweed *Potamogeton pectinatus* may show a high degree of phenotypic plasticity in the burial depth of wintering tubers in response to grazing pressure by swans in shallow lakes (Hidding, Nolet, van Eerden, Guillemain, & Klaassen 2009). Here, herbivore avoidance is traded off against competitive strength, as deeper buried tubers escape swan herbivory but face higher energy demands during sprouting (Santamaría & Rodríguez-Gironés 2002). As a consequence of deeper burial, survival of tubers in locations with high swan densities may increase, contributing to the persistence of aquatic vegetation and to the interaction between herbivore and plant. Although phenotypic plasticity can evidently affect population and community dynamics, it has long been neglected in modelling approaches. However, ignoring phenotypic plasticity may lead to qualitatively misleading results. For example, the perceived balance between competitive and facilitative interactions could be shifted (Callaway, Pennings, & Richards 2003). Consequently, a few recent models incorporate phenotypic variability and assess its effects, e.g. on intraspecific competition among herbaceous plants (Brison & Reynolds 1997), trees (Hauhs, Kastner-Maresch, & Rost-Siebert 1995), or animals (Wichmann, Groeneveld, Jeltsch, & Grimm 2005). So far, most of these models use new theoretical approaches that still have to be validated with empirical data. Therefore, we consider it an important next step to strengthen the link between experimental data on plastic responses and models addressing variability among phenotypes.

Species

Species identity is probably the most commonly used aggregation criterion in ecological studies (for a review of the species concept see Claridge, Dawah, & Wilson 1997). For instance, the great majority of approaches assessing biotic interaction strength are based on the species concept (see Wootton and Emmerson (2005) for a review). Another example where 'species' is the focal aggregation type is coexistence theory. Theoretical work on coexistence of competing species has suggested two opposing theories: coexistence through stabilizing mechanisms or through fitness equivalence. With fitness equivalence, individuals do not necessarily differ (Chesson 2000), so that a corresponding coexistence model only needs to account for different species identities. In contrast, when stabilizing mechanisms are assumed, individuals differ in a number of properties at the species level (Chesson 2000). When the function in the community is important, functional types should be used, because species richness is not a good surrogate for functional richness (Díaz & Cabido 2001). However, the species level should be used when species are not redundant. A field study on facilitation networks showed that, far from being redundant, single species belonging to the group of benefactors may act synergistically, resulting in a cascade of positive interactions (Altieri, Silliman, & Bertness 2007). In general, when considering a range of dependent variables instead of restricting investigations to a single variable, the detected redundancy is often much lower (Gamfeldt, Hillebrand, & Jonsson 2008). Therefore, when investigating a number of characteristics of natural communities without focusing on a specific aspect, the species level may be superior to a functional type approach.

Functional types

The concept of functional types is probably the most flexible aggregation, because it may be defined with respect to any function of the study objects. The functional type concept has been discussed as a convenient method for grouping species and reducing complexity (Wilson 1999; Solomon & Shugart 1993). This functional approach is based on the concept that species within groups might fulfill the same function in a given system and thus would be redundant (Walker 1992) or ecologically equivalent (Solomon & Shugart 1993). Reducing complexity is not the only advantage of the functional type approach. With a functional type approach, trait convergence and divergence can be determined in local communities and the importance of different community assembly rules such as habitat filtering and limiting similarity can be assessed (Grime 2006). Both experiments (Fukami, Bezemer, Mortimer, & van der Putten 2005) and observational studies (De Bello, Lepš, & Sebastia 2006) aiming at a better understanding of community assembly have shown that functional diversity can vary independently of species diversity. Fukami et al. (2005) showed that community assembly was simultaneously driven by trait-based assembly rules (trait convergence) and species-level priority effects (species divergence). Another advantage of a functional type approach is its ability to integrate those functional traits that determine the response of a community to environmental change (response traits) and those functional traits that influence the effect of environmental change on ecosystem processes (effect traits) into a common framework (Suding et al. 2008). This is important as there is a growing consensus that functional diversity rather than taxonomic diversity strongly determines ecosystem functioning (Díaz & Cabido 2001). Functional type approaches have the disadvantages, that it is not always clear which traits are most relevant for assembling the functional groups and that they require large amounts of data.

Trophic guilds

Aggregating individuals according to similar trophic status has been used extensively to describe faunal community structure, particularly in arthropod and aquatic ecology (e.g. Vander Zanden & Rasmussen 1996). The trophic guild concept is similar to the functional type concept but restricted to animals. Examples for systems where trophic guilds are relevant are relationships between trophic guild identity of forest litter fauna and community management status (Moreno, Guevara, Sanchez-Rojas, Tellez, & Verdu 2008) and interactions between trophic guild identity of fish and invertebrates (Flecker 1992). In contrast to trophic guilds, trophic levels do not represent aggregation types in themselves, but can be represented by different aggregation types such as species or body size class. Trophic guilds may react differently to environmental conditions, which may feed back on individual-level interactions such as competition (Fritz, Duncan, Gordon, & Illius 2002). This illustrates potentially confounding effects of the classification into trophic guilds on conclusions at the community level. Nevertheless, aggregation into trophic guilds can provide a first indication of relevant community processes (Moreno et al. 2008) and guide the prioritisation of subsequent less aggregated studies.

Body size classes

Body size is a phenotypic trait of plant and animal individuals and a main driver of energy flow at the individual level, affecting individual metabolism and resource uptake according to well defined quantitative laws on the one hand (Brown, Gillooly, Allen, Savage, & West 2004) and individual resource perception and spatial behaviour on the other hand (Haskell, Ritchie, & Olff 2002). In spite of the doubts raised by Kozlowski and Konarzewski (2004), body size distribution, i.e. the partitioning of individuals into body size classes at both the population and community level, is becoming a common way to describe population and community structure (Enquist et al. 2007). Body size distributions, being directly linked to resource availability and energy flow, were observed to be relatively invariant when compared to taxonomic composition and vary more consistently along environmental gradients (Sabetta, Basset, & Spezie 2008). Body size distributions are also used to describe distributional patterns, including patterns of matter and energy allocation within networks (Woodward et al. 2005). Using data from natural food communities, Otto, Rall, & Brose (2007) showed that body size relationships are related to the stability of food webs. Breaking down community-level distributional patterns into body size-dependent processes at the individual level requires knowledge on how interactions among individuals mediate the simple up-scaling of metabolic laws from the individual to the community level. In line with this, body size has been found to play an important role in coexistence and community organization (Basset & DeAngelis 2007). The development of a metabolic theory of coexistence is a major challenge to the scaling process of body size-based data in community ecology (Ings et al. 2009).

Choosing a type of aggregation

In his seminal paper, Levin (1992) states: ‘We must learn how to aggregate and simplify, retaining essential information without getting bogged down in unnecessary detail’. Not more, not less is the task when choosing a type of aggregation for a study. As a first approach to solve this task and identify appropriate aggregation types, we propose a three-step procedure (Fig. 3):

1. Decide, which *processes* may be relevant for the population- or community-level patterns to be explained.
2. Select *properties* that describe the processes adequately and use them as aggregation criteria to determine the corresponding *aggregation types*.
3. Derive appropriate *study objects* from the set of properties.

The first two steps are the two most crucial ones, since they constitute the actual process of aggregation from natural complexity to essential information. Starting with the *selection of processes* accounts for the fact that the ecological processes themselves drive all dynamics and generate all patterns that we observe at the community level (*sensu* Levin 1992). Following the principle of parsimony, the aim is to include all processes that show variability significantly influencing the target patterns and dynamics but ignore those that appear to be of minor importance. However, whenever predicting target patterns and dynamics under future conditions or in different regions, we need to be careful because processes of minor importance under current conditions may contribute to significant trends in patterns under new conditions. One possible solution is to test our chosen set of properties and processes at different points in time or space (Graf, Bollmann, Suter, & Bugmann 2005; Garzon, de Dios, & Ollero 2007). Whenever these test data are not available it should at least be discussed why stability of processes over time and space is assumed.

In principle, it is not possible to know whether a particular process is relevant for the outcome of our study or not, unless we explicitly investigate the process in question. However, in most cases, it is not possible to do that. Nevertheless, we implicitly or explicitly make decisions on which processes to include in *every* study. Therefore, we should explicitly explain the choice. One option is to transfer knowledge from other study systems; another option is to use ecological expert knowledge and our trained intuition to narrow down the potential range of ecological processes. In practice, that means building up knowledge and collecting information on related studies and study systems. For instance, to identify important processes in the grassland productivity example from the introduction of this paper, we could first apply textbook knowledge and assume that resource uptake and inter-individual interactions are important processes, because they drive growth, reproduction and mortality of the plants (Fig. 3). Additionally, we know from recent case studies that nitrogen fixation by symbioses between legume species and rhizobia may affect the outcome of the study (van der Heijden et al. 2006; Kempel et al. 2009). In a few cases, we may have the resources to explicitly check *a priori* whether processes have an effect on the outcome of the study. This emphasizes the importance of pilot studies, which have been used in ecology for a long time to determine appropriate sample sizes and influential experimental factors. The selection of the processes does not necessarily mean that we have to study them explicitly in our target study. Instead, we can often capture the process by including the relevant properties and their effects on the outcome of the study but treat the process itself as a black box.

Once we have decided which processes to consider, the next step is the *selection of the properties* that drive the identified key processes. Properties can be selected from the set of properties associated with the processes selected in the previous step (Fig. 1). Again, as in the step of selecting relevant processes, we need to come back to our ecological knowledge and intuition. We first need to decide how accurate our results should be, i.e. which minimum effect size we want to be able to detect. By comparing these minima with available data on effect sizes of aggregation type properties from (pilot) studies at different levels of aggregation, we can identify the relevant properties for our study. For example, in the case study on grassland productivity, it is clear that productivity depends on nitrogen fixation (Fig. 3) which in turn depends on the presence of legumes. Hence, we need at least a distinction between leguminous and non-leguminous individuals. We further know that different legume species build symbioses of different strength and differentially contribute to grassland productivity (Sprent & Sprent 1990). Therefore, considering the property ‘species identity’ may be crucial. We know that the ability to form a symbiosis can also vary between genotypes of both legumes and rhizobia (Bourion et al. 2007). However, when considering the effect size of the influence of different genotypes and comparing the potential impact on the overall productivity of the grassland with the

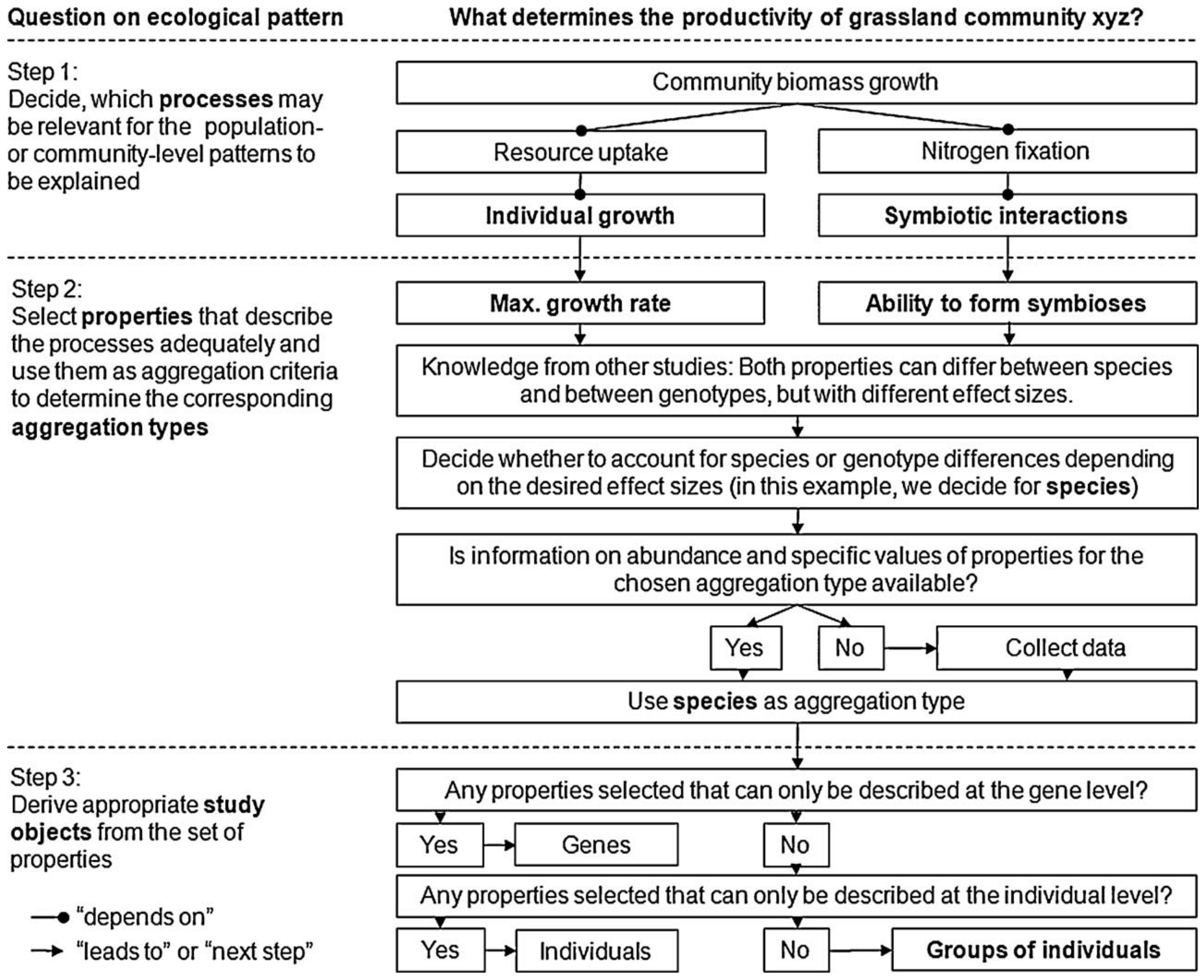


Fig. 3. Overview of the three-step-procedure linking ecological question, processes, properties, aggregation types, and study objects including an example application to the investigation of grassland productivity (example-specific decisions highlighted in bold fonts in the right-hand column of the figure).

desired accuracy of the result, we may decide to omit this additional detail (Step 2 in Fig. 3).

We obtain the *type of aggregation* using the selected properties as aggregation criteria. For example, if we want to account for the species-specific ability of individual plants to form symbioses then the type of aggregation should be the species. If genetic variability matters – as it is likely in dominant and foundation species (see Section 'Genotypes') – the genotype is the appropriate aggregation type. To assess the management status of a forest, it can be sufficient to consider trophic guilds in the litter (see Section 'Trophic guilds'). The stability of food webs may be assessed by investigating body size class hierarchies (see Section 'Body size classes'). Coming back to the grassland productivity example, the majority of studies have used species as aggregation type, while sporadically, when the focus was on interactions or nitrogen fixation, functional types, trophic guilds, or genotypes have been used.

The *decision on the study objects* is a more methodological and practical decision but arises similar to the type of aggregation from the relevant set of processes. Defining the study objects limits the possibilities of how detailed the system can be described. For example, working on the level of groups of individuals does not allow an explicit study of inter-individual interactions. However, in the procedure that we suggest, this decision is already made in the first step, where the relevant processes (including interactions) are identified.

Conclusions

When predicting population and community dynamics, aggregation is crucial to make efficient use of the available resources. However, the type of aggregation such as species, genotype, or functional type is not given *a priori*. Rather, the aggregation type should be chosen carefully according to the aims of the study and existing knowledge on important ecological processes and properties of the study objects. We have proposed a framework linking study objects, their properties and associated ecological processes to derive the corresponding aggregation types and have presented a first heuristic strategy to choose aggregation types. In most cases, this choice is neither easy, nor straightforward due to the lack of relevant data. This is even more apparent when predicting population and community dynamics under changing environmental conditions. Moreover, in some cases, it may be necessary to address more than one aggregation type at once to explain a particular phenomenon. For instance, investigating succession at the species level has shown divergence over time while using the functional type level resulted in convergence (Fukami et al. 2005). Hence, the collection and synthesis of data on the relationship between aggregation types and population and community dynamics is pivotal and should be intensified. Enhanced collaboration between modelers and empiricists may contribute to this aim. For example, the combination of simplified empirical pilot studies and more complex model predictions may provide *a priori* insights into the relative importance of ecological processes (Meyer, Mooij, Vos, Hol, & van der Putten 2009). A more specific approach would be to apply pattern-oriented modelling approaches that rely on the comparison of simulated and empirical patterns to calibrate model parameters (Grimm et al. 2005). The resulting models may then be used to assess the importance of different ecological processes or properties. In any case, we call for a clear statement explaining the choice of the aggregation type in each study of population or community dynamics.

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