Ecotoxicology and macroecology – Time for integration

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ABSTRACT

Despite considerable progress in ecotoxicology, it has become clear that this discipline cannot answer its central questions, such as, “What are the effects of toxicants on biodiversity?” and “How the ecosystem functions and services are affected by the toxicants?”. We argue that if such questions are to be answered, a paradigm shift is needed. The current bottom-up approach of ecotoxicology that implies the use of small-scale experiments to predict effects on the entire ecosystems and landscapes should be merged with a top-down macroecological approach that is directly focused on ecological effects at large spatial scales and consider ecological systems as integral entities. Analysis of the existing methods in ecotoxicology, ecology, and environmental chemistry shows that such integration is currently possible. Therefore, we conclude that to tackle the current pressing challenges, ecotoxicology has to progress using both the bottom-up and top-down approaches, similar to digging a tunnel from both ends at once.

Keywords:
Environmental toxicology
Macroecology
Biodiversity
Large spatial scale
Ecological impact assessment

The essence of the ocean cannot be seen in a drop of seawater
Kurt Tucholsky, 1925

1. The central questions in ecotoxicology remains to be answered

Currently ecotoxicology represents a distinct scientific field that investigates impact of chemical contaminants on the environment at the molecular, physiological, individual, and ecological levels. This discipline is characterized by rapid progress and many remarkable achievements. However, a strategically critical issue is now becoming apparent, as to whether we have really solved the deep, chronic, and relevant problems regarding contaminants. The answer, if taken seriously, is discouraging. The ultimate aim of ecotoxicology is to determine and predict the effects of contaminants in real-world systems at large spatial scales (e.g. Newman and Unger, 2003). However, our capacity to elucidate and predict such effects remains severely limited. For example, with respect to four areas of active investigation and discussion in ecotoxicology, the following central questions have not been answered so far:

- What are the effects of toxicants on biodiversity and ecosystem goods and services? What is the impact of modern compounds that are currently used in normal practice (i.e. not due to accidents and violation of the application norms)?
- What is the contribution of chemical toxicants to the degradation of coral reefs like the Australian Great Barrier Reef?
- What are the effects of pharmaceuticals on biological communities, ecosystems, and their functions, goods, and services?
- What are the large-scale effects of oil spills on marine and coastal ecosystems?

In our opinion, these different examples illustrate a single general problem; namely, the lack of current capacity to assess and predict the effects of toxicants on real-world ecosystems at large spatial scales. In this situation, decisions in the risk assessment are made under conditions of deep uncertainty. As a result, the protective standards that are prescribed are either over- or under-protective, which in turn leads to economic inefficiency or environmental hazards, respectively. Furthermore, attempts to manage landscapes efficiently, to implement conservation measures, and to place an economic value on ecological impacts, are impaired deeply.

The major cause of this central problem is that ecotoxicology and ecological risk assessment are based almost exclusively on a single paradigm, namely, a bottom-up approach that implies the use of toxicity tests carried out at the (sub)organism level (Box 1) and also, to a lesser degree, experiments on simple artificial ecosystems whose purpose is to predict the effects of contaminants on real-world ecosystems and entire landscapes. Even the most advanced current initiatives, such as REACH or the new “EU directive concerning the placing of plant protection products on the market”, do not base their predictive methods on the empirical...
knowledge about the effects of contaminants on real-world ecosystems and landscapes. Rather, the risk assessments are based on extrapolation from organisms to ecosystems and from small-scale systems to large-scale systems. The validity of these methods of extrapolation have been extremely rarely tested in a systematic manner. In ecology, an approach that seeks to develop understanding of ecological systems through the components of these systems. In this approach, patterns, processes, and mechanisms elucidated at small scales are used to describe and predict large-scale systems and processes (Gaston and Blackburn, 2000).

Top-down approach — in ecology, an approach that seeks to develop understanding of ecological systems by investigating the properties of such systems in their entirety. The main rationale for this approach is based on the fact that complex systems, such as biological communities and ecosystems, may exhibit properties that arise from the interaction of their constituent parts, and therefore are poorly predictable from the knowledge about these parts considered separately (Gaston and Blackburn, 2000).

Macroecology — the subfield of ecology that studies relationships between organisms and their environment at large spatial and temporal scales to characterize and explain patterns of abundance, distribution and diversity (Brown and Maurer, 1989; Brown, 1995; Gaston and Blackburn, 1999, 2000). Macroecology employs top-down holistic approach combined with correlational statistical framework, mathematical modeling, and to a much smaller degree experimental methods (Blackburn, 2004; Kerr et al., 2007).

It is not the bottom-up approach itself the cause of the problem. The approach has an important role to play. Rather, the problem results from the insufficient development of a complementary top-down approach that is focused on ecological effects at large spatial scales (Fig. 1). The bottom-up approach is an important tool that is indispensable for the investigation of many issues related to the regulation and risk assessment. However, after more than 50 years of development of ecotoxicology, it has become clear that this single tool, albeit a very good one, is insufficient to meet all the relevant challenges.

2. How ecology is solving large-scale problems

In ecology, the top-down approach, which considers large-scale systems as integrated entities, was re-established at the end of the 1980s in the form of macroecology (Brown and Maurer, 1989: Box 1). Macroecology combines the “old-school” observational approach, which had appeared before any formal science was established, with novel and sophisticated statistical methods and modelling (Blackburn, 2004). The main reason that these methodologies were combined, in what may be called the “macroecological approach”, was the basic inability of small-scale bottom-up studies to analyse and predict large-scale ecological patterns, similar to the current case with ecotoxicology. The holistic top-down approach adopted by macroecology suffered from no such problems (Box 1). It enabled the discovery of regularities in large-scale patterns that only appear at large spatial scales and are stochastic and undetectable from the local perspective (Brown, 1995; Maurer, 1999; Kerr et al., 2007). This made macroecology an outstanding ecological subdiscipline.

The establishment of macroecology was accompanied by heated debates because, after decades in which the bottom-up reductionist approach predominated, many ecologists were preconditioned to believe that this was the only relevant approach to ecology and science in general (Gaston and Blackburn, 1999). However, the top-down macroecological approach has rapidly shown itself to be a credible predictive scientific practice, and, at present, macroecology is used to make large-scale (on the scale of landscapes to continents) predictions of diversity, species distributions, and other patterns (e.g. Blackburn, 2004; Kerr et al., 2007). For example, accurate predictions of the species diversity alterations induced by climate change and human population have been made and confirmed for European birds and Canadian butterflies using historical data on the climatic and biotic changes that occurred during the twentieth century (Evans and Gaston, 2005; White and Kerr, 2006, 2007).

3. What ecotoxicology can learn from macroecology

Ecotoxicology, and science in general, can learn much from this recent historical development in the field of basic ecology. To be able to tackle large-scale problems, ecotoxicology should, in a similar manner to basic ecology, develop a holistic top-down approach, which could be termed a “macroecological approach in Ecotoxicology”. This approach should include the assessment of exposure to and the effects of toxicants in real-world systems.
Box 2. Future research directions for a macroecological approach in ecotoxicology

To go beyond the question “How can we realistically predict the ecological effect of a certain toxicant without empirical dose–response data from real-world ecosystems?” to ask “How can we derive dose–response data from observations of real-world ecosystems in order to predict such effects?”

In the top-down approach, the uncertainty associated with the complex and variable character of ecosystems is assumed to be manageable, and dose–response data are derived by extracting them from the complex relationships between the environment and biota. The methods used for this purpose include trait-based stressor-specific descriptors, advanced factor-isolating statistics, and integrative observational-experimental techniques (Box 3).

To go beyond the question “What is the sensitivity of a certain species or taxonomic group to a certain toxicant?” to ask “What is the sensitivity of a certain type of community or particular ecosystem function and service to a certain toxicant?”

From the top-down perspective, it is natural to consider a community or an ecosystem as an integrated system that can be characterised by a certain sensitivity to chemical stressors. This approach yields sensitivity values at the system level that are habitat-specific and cover both indirect effects of contaminants and the influence of environmental stressors. The approach contrasts with the currently prevailing method of assessing community and ecosystem sensitivity, which involves the analysis of the sensitivities of selected species present in systems or their analogues (e.g. a species sensitivity distribution approach).

To go beyond the question “How many and which species can be/are affected by a certain toxicant?” to ask “What are the biological and ecological traits, ecosystem functions, goods, and services that can be/are affected by a certain toxicant?”

To understand the effects of chemical toxicants on biodiversity at a level that allows realistic predictions of those effects to be made, it is necessary to understand the underlying ecological mechanisms that can be translated into biological and ecological traits and ecosystem functions. Furthermore, knowledge about the state of ecosystem functions and services has direct relevance for practice, due to the common protection goals and economic value. Therefore, a focus on traits, and ecosystem functions and services is indispensable for both the diagnosis of and prognosis for the state of the environment.

To go beyond the question “How should a certain non-chemical abiotic or biotic (stress) factor be considered in ecological risk assessment?” to ask “What is the actual ecologically acceptable concentration of a certain toxicant for a certain type of ecosystem, taking into account the combination of environmental (stress) factors that are actually present in this ecosystem type?”

It is impossible in practice to assess and predict the ecological effects of interactions among certain contaminants and abiotic or biotic (stress) factors using the experiment-based bottom-up approach, due to (i) the overwhelming number of factors and their possible combinations, and (ii) the interdependence of the factors. In contrast, the top-down approach focuses the assessment on the concrete and relevant combinations of (stress) factors that are actually present in a certain system and is the most practical way to deal with the ecological effects of multiple factors.
By Gestel, 2008). However, regarding the current complex chemical contamination, such field–ecology approaches have been criticised frequently and implemented rarely (Fig. 1), due to such complications as confounding factors, multiple exposures, diffuse non-point contamination, time-variable contamination, ecological complexity, and biological variability over time and space. All these issues present strong challenges to the identification of a causal relationship between exposure to contaminants and ecological impairments, and are appealed to frequently in arguments to the relationship between exposure to contaminants and ecological issues present strong challenges to the identification of a causal relationship between exposure to contaminants and ecological impairments, and are appealed to frequently in arguments to the effect that it is impractical, if not impossible, to investigate the ecological effects of a certain contaminant or type of contaminant in real-world systems. Furthermore, the predictive abilities of ecology in general have frequently been called into question (Lawton, 1999; Ghilarov, 2001; McGill et al., 2006).

4. How can ecotoxicology adopt the top-down macroecological approach

Despite the difficulties described above, there are clear signs that the macroecological approach can be established to deal with large-scale effects of toxicants. The major preconditions for the introduction of this approach into ecotoxicology are the progress and new developments in the following three fields: (i) ecology, (ii) field ecotoxicology and bioassessment/biomonitoring, and (iii) environmental chemistry and exposure assessment (Box 3). Why such advances and developments are necessary, can best be explained in terms of their ability to overcome the major obstacles that hinder the assessment and prediction of the effects of toxicants at large spatial scales. There are four such obstacles:

- The challenge of inferring the causal connection between exposure to toxicants and ecological impairment in the presence of confounding factors and natural variability, and at spatial scales at which the experimental testing of hypotheses is impractical and/or unethical;
- The challenge of assessing the exposure, modelling, and expressing the general toxicity of contaminated environmental media;
- The challenge of making ecological predictions at large spatial scales;
- The lack of a comprehensive conceptual framework for the assessment and prediction of the effects of contaminants at broad spatial scales.

The advances and developments that could enable these specific challenges to be overcome are reviewed and discussed below.

4.1. The challenge of identifying causal relations

The following factors can cause difficulties in determining whether exposure to contaminants causes ecological impairment: (i) pronounced natural variability that is especially high at large spatial scales (e.g. differences in species composition between regions) and (ii) natural and anthropogenic confounding factors (e.g. changes in hydromorphology) that mask the effects of contaminants. An additional difficulty is that it is frequently not, for practical and/or ethical reasons, possible to test hypotheses that pertain to large spatial scales by doing experiments, yet it remains inappropriate to extrapolate from small-scale experimental systems to large spatial scales (Blackburn, 2004; Kerr et al., 2007; Suter, 2007; Rohr et al., 2006, 2008) (but see below about large-scale experiments). Current promising approaches to overcoming this challenge include the following: (a) statistical methods, (b) trait-based methods, and (c) integrative observational-experimental approaches. These approaches are described in greater detail below.

The statistical techniques that have been developed for ecological research at large spatial scales include a wide array of multivariate methods designed to isolate factors of interest by analysing observational data, rather than by conducting experiments, and thus to provide in-depth understanding of the observed patterns (e.g. Brown, 1999; Kerr et al., 2007; Gotelli et al., 2009). These techniques include variance partitioning, path analysis, partial ordinations, and the forward selection of predictors (e.g. Borcard et al., 1992; Leps and Smilauer, 2003). In addition, the frequent absence of controls or reference points in natural systems has stimulated the development and application of case- and system-specific null-hypothesis models (e.g. Blackburn, 2004; Ulrich and Gotelli, 2007; Béketov, 2009). These statistical methods, together with the confirmation of patterns that have been observed across spatial regions and over time, natural experiments, and process-based models, currently represent the essence of the hypothesis-testing experimental approach within the observation-based macroecological framework (Blackburn, 2004; Kerr et al., 2007).

The trait-based methods comprise a wide array of techniques for the description and analysis of biological systems. The term ‘trait’ refer to ecological, biological, and other attributes of taxa (e.g. breathing type, feeding type, propensity for dispersal, and duration of life-cycle). The description of biological communities in terms of

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**Box 3. Major preconditions for the establishment of the macroecological approach in ecotoxicology**

**Progress in ecology** — Macroecology emerged at the end of the 1980s and has been increasingly successful in evaluating and predicting ecological patterns at large spatial scales. Theoretical ecology developed several concepts that have the potential to improve the predictive capacity of ecology and are particularly relevant for the assessment of large-scale effects. These concepts include the habitat template concept and the functional trait research program, for which counterparts have already been developed in applied research to detect and quantify the effects of pesticides at large spatial scales. Other notable theoretical advances that are relevant for this analysis include the metacommunity concept and the stochastic niche theory. For example, the question, “What role do contaminants play in exacerbating the vulnerability of indigenous communities to invasive species?” can be answered at the theoretical level by the stochastic niche theory.

**Progress in field ecotoxicology and bioassessment/biomonitoring** — The most important developments that have enabled researchers to tackle the problem of identifying causal relations between exposure to contaminants and ecological impairment include the following: trait-based methods and stressor-specific community descriptors, statistical methods designed to isolate factors of interest non-experimentally, and various integrative observational-experimental approaches.

**Progress in environmental chemistry and exposure assessment** — The most important developments include the following techniques: advanced sampling methods such as event-driven and passive sampling techniques, which are designed to overcome problems of pulse and time-variable exposure; advanced analytic methods and extraction techniques that utilise new compounds and heterogeneous media; and large-scale exposure models (e.g. GIS exposure models).
traits, which represents the basic ecological view of such systems, can provide a more complete, yet at the same time simplified, description of the systems than can the taxonomic view (McGill et al., 2006). In bioassessment (or biomonitoring), traits provide a wide range of tools and indices that are relatively specific to stressors and independent from confounding factors in comparison to traditional taxonomy-based metrics (e.g. Beketov and Liess, 2008a). In addition, the use of traits is not constrained by geographical and geomorphological factors and associated differences in biological communities (Statzner et al., 2001; Schlatter et al., 2010). Furthermore, traits provide measurements that are related to function and are relevant for the assessment of ecosystem processes and services (Lecerf et al., 2006). The recent comprehensive review by Bonada et al. (2006) showed that, in freshwater bioassessment, trait-based metrics are very close to an ideal monitoring tool that can be characterised by the following features: 1) derived from sound ecological theory; 2) a priori predictive; 3) having the potential to assess ecological function; 4) having the potential to discriminate between different types of human impact; 5) having low costs for sampling, experimentation, and taxonomic identification; 6) involving simple sampling protocols; 7) being applicable to large scales (across ecoregions or biogeographic provinces); and 8) providing a reliable indication of changes in overall human impact. More recently, studies that used the trait-based bioindicator system SPEAR (www.systemecology.eu/SPEAR/Start.html) have shown that SPEAR indicators have superior specificity to stressors such as pesticides (Liess and von der Ohe, 2005; Liess et al., 2008) and other organic toxicants (Beketov and Liess, 2008a) than other existing indices. It was also shown that these indices can be applied to biomonitoring data at the family level, which makes this tool cost-effective and applicable for routine monitoring programs in many countries. As a consequence, the index SPEAR stated by Liess and Liess (2008) was suggested as a Europe-wide bioindicator of pesticide contamination in rivers and streams (Anonymous, 2009; Beketov et al., 2009). Despite all these promising features, the trait-based methods are obviously not disentangle effects of all the stressor combinations, particularly when applied without other methods (e.g. experiments). For example, as any correlative approaches, they can be inefficient for strictly inter-correlated stressors and stressors having the same modes of action.

The integrative observational-experimental approaches constitute a diverse set of investigatory tools and methods, and represent a combination of the top-down and bottom-up approaches. The major strength of the experimental studies is the potential to provide unequivocal evidences for the investigated cause–effect relations. Therefore such studies can be used to test hypotheses generated by top-down investigations and disentangle effects of multiples stressors (e.g. pesticides and hydrodynamic stress from agricultural surface water run-off, Liess and Schulz, 1999). Thus, in bioassessment and retrospective risk assessment, various experimental approaches are used frequently to confirm hypothesized causal relations between exposure to contaminants and biological impairments. For example, this approach is represented by the TRIAD concept, which refers to the simultaneous application of in vivo and in vitro bioassays together with chemical analysis and sampling of communities (Chapman, 1990; Chapman and Hollert, 2006). TRIAD involves three complementary lines of investigation: (i) analytical chemistry to quantify pollution, (ii) bioassays to quantify toxic effects, and (iii) in situ biological assessment to quantify alterations in communities. This combination enables the effects of exposure to multiple contaminants and additional stressors to be elucidated.

Experimental studies that use small-scale model systems (mesocosms or model ecosystems) allow the effective elucidation of the mechanisms that underlie large-scale processes, such as recovery and recolodisation (e.g. Caquet et al., 2007; Beketov et al., 2008; Liess and Foit, 2010), and the propagation of effects through different levels of biological systems (e.g. Van Wijngaarden et al., 2005; Beketov et al., 2008; Rohr et al., 2008; Foit et al., 2010). For example, it has been shown that recovery after contamination depends strongly on intraspecific competition (Liess and Foit, 2010), the composition of the community in terms of life-cycle traits (Beketov et al., 2008; Liess and Beketov, 2011) and the isolation of the affected community (Caquet et al., 2007). With regard to the propagation of effects, as mentioned above, Rohr et al. (2008) showed that a toxicant at a concentration that has been found to be safe in laboratory tests can affect amphibians in field conditions when parasitic infection is present. Similarly, heavy metals, food shortage, and exposure to UV-radiation showed combined effects on Antarctic amphipods with large-scale implications (Duquesne and Liess, 2003).

Although it is generally considered unethical to perform experiments with large-scale systems such as a stream or a landscape, some experimental work with such systems may be well justified. For example, when the current risk assessment has deemed a particular concentration of a chemical to be environmentally safe, it would be more ethical to test these assessments in a limited region rather than allow the widespread release of the chemical. Such large-scale experiments can be further elaborated locally by artificial exclusion of confounding factors (e.g. hydrodynamic stress, Liess and Schulz, 1999) and can provide invaluable information for the validation of the ecotoxicological risk assessment.

4.2. The challenge of assessing the exposure, modelling, and expressing the general toxicity

Reliable assessment of the chemical exposure is indispensable for understanding the large-scale effects of toxicants. For example, the studies by Gibbs et al. (2009) and Geiger et al. (2010) have recently identified biodiversity impacts in relation to agriculture, but these impacts cannot be unequivocally linked to the agrichemicals due to the lack of measured chemical exposure. The challenge of exposure assessment, modelling, and generalised toxicity expression of mixtures of multiple contaminants is caused by the enormous diversity of chemical contaminants that are present in the environment (Schwarzenbach et al., 2006), as well as their spatial (Beketov and Liess, 2008b) and temporal variability (Guo et al., 2004). To assess exposure at large spatial scales, new methods of sampling and analysing multiple (mainly organic) compounds are being developed continuously. Understanding spatial variability requires extensive sampling programs at different spatial scales, from within a river channel (Beketov and Liess, 2008b) to between biogeographical regions (Schafer et al., 2007). With regard to temporal variability, promising methods include (i) the use of passive samplers (which accumulate certain organic compounds and are useful for investigating time-variable and pulse exposures; e.g. Schafer et al., 2008), and (ii) the use of event-controlled and sediment-trap samplers (which collect water during increased run-off to sample contaminants associated with run-off, Liess et al., 1999). Additionally, basic patterns and mechanisms of the toxicants’ effects at large spatial scales can be investigated using contaminants with stable exposure as model toxicants (e.g. salinity or metals in sediments, Keeford et al., 2011).

With regard to the modelling of exposure to contaminants at large spatial scales, the meso- and macroscale GIS-based models are important tools for the assessment and prediction of ecological effects and risks. One example that is particularly relevant to the
proposed macroecological approach is the EU-scale model of pesticide run-off into streams and the ecological risks associated with this run-off (Schriever and Liess, 2007; Schriever et al., 2007). This model, which is based on land use, precipitation, slope, and soil properties, shows the potential effects of pesticide input into water at the EU scale. It has been validated in three biogeographical regions of Europe (Schäfer et al., 2007; Liess et al., 2008).

With regard to generalised toxicity expression of mixtures of multiple contaminants, a promising approach that has been found to be reliable in large-scale studies is the standardization of measurement in terms of toxic units (TU). This approach involves the uniform expression of concentrations, not in the usual mass-per-volume units (e.g. μg/l), but instead in terms of their toxicity to standard test organisms (i.e. in TUs). TUs are calculated as the logarithmic ratio of environmental concentrations to values of EC50 or LC50 (the concentration that affects or kills 50% of test organisms, respectively) for standard test organisms (for invertebrates – *Daphnia magna*, for algae – *Selenastrum capricornutum*, and for fish – *Pimephales promelas*).

4.3. The challenge of making ecological predictions at large spatial scales

Predicting ecological effects at large spatial scales is challenging due to (i) limited recent and historical data that hinder calibration and validation of the predictive methods (Algar et al., 2009), and (ii) our still poor understanding of the large-scale processes and mechanisms, which result in highly divergent predictions made by different methods even when their accuracy appear excellent (Araujo and New, 2007). In our opinion, predicting large-scale ecological effects of toxicants can profoundly benefit from adopting and developing predictive models that have been created by researchers in macroecology and related ecological disciplines. Such models have been developed (largely in two recent decades) to predict the effects of climate change on biodiversity and have the potential to be applied to different types of stressors, including contaminants (this however will require serious further work, to consider toxicant-specific issues, e.g. Liess et al., 2008; Kattwinkel et al., 2011). These models can be divided roughly but usefully into two categories: 1) niche-based models and 2) environment-richness regressions (Algar et al., 2009). The niche-based models describe and model the niches of species from point observations and project these models forward using future climate scenarios or other conditions. The environment-richness correlations are based on the direct link between environmental factors and taxonomic richness that can be elucidated by macroecological studies without an explicit description of niches for individual species (Currie, 1991; Hawkins et al., 2003; Algar et al., 2009). These two basic categories of model cover a highly diverse range of techniques, and there are more that cannot be classified clearly in accordance with this system. The techniques include such widely used methods as climate envelopes (e.g. Beale et al., 2008; Araujo et al., 2009), artificial neural networks (e.g. Pearson et al., 2006), trait-based prediction methods (e.g. Bonada et al., 2007; Liess et al., 2008; Hering et al., 2009), regression models (e.g. generalised linear and generalised additive linear models; e.g. Araujo et al., 2005), classification tree analyses (e.g. Prasad et al., 2006), mechanistic simulation models (Gotelli et al., 2009), casual modelling and path analysis (Shipley, 2009), and many other methods. Comparison of different models has shown that their predictions can vary considerably (Pearson et al., 2006). To tackle this problem, the ensemble forecasting framework was proposed. This approach combines predictions from multiple models and sophisticated analyses of multiple results and delivers much more robust forecasts than the use of a single model (Araujo and New, 2007).

4.4. The lack of a comprehensive conceptual framework

A comprehensive conceptual framework for the assessment and prediction of the effects of contaminants at broad spatial scales has not been developed previously because (i) chemical contaminants are rarely considered in theoretical and basic ecology (Rohr et al., 2006), and (ii) ecotoxicological concepts, which have been historically originated from human toxicology, are still mainly oriented on the (sub)organism-level effects (Van Straalen, 2003). The challenge posed by the lack of such a framework can be overcome by applying the theoretical background and methodology developed by macroecology and ecology in general (Box 3).

Among recent theoretical advances, perhaps the most influential is the metacommunity concept (Leibold et al., 2004), which was preceded by the well-known theory of island biogeography (MacArthur and Wilson, 1967), as well as by pioneering work by Thienemann (1918) who outlined the concept of species-area and environment–trait relations. In contrast to much formal community theory, which assumes that local communities are closed and isolated (e.g. Lotka–Volterra equations), the concept of the metacommunity considers communities as parts of a larger system, which are linked by the dispersal of multiple interacting species. In their seminal paper (Leibold et al., 2004), the authors reviewed the concept of the metacommunity and defined four basic paradigms that describe metacommunities: the patch–dynamic, species-sorting, mass-effect, and neutral paradigms. Regarding chemical contaminants, these paradigms are crucial to our perception of the effect–recovery mechanisms at large spatial scales, as they can interlace toxicants’ effects with other relevant processes (e.g. link the post-contamination recovery with species dispersal and migration).

Another important theoretical advance is the stochastic niche theory, which is based on neutral theory and tradeoff–based niche theories (the species-sorting paradigm, according to Leibold et al., 2004). This theory links stochastic processes to competition for resources, invasions, and the assembly of communities (Tilman, 2004). The stochastic niche theory predicts that periodic disturbances (which can be a pesticide pulse if we apply it to ecotoxicological issues) allow species to overcome limits on recruitment that depend on resources and therefore to increase species diversity at the local level. In addition, this theory explains the mechanisms of species invasions and enables the invasion paradox that is observed in some studies (negative correlation between diversity and invasions) to be resolved. Therefore, it is useful for understanding the role of contaminants in the occurrence of species invasions.

Another important complex of concepts includes the habitat template concept (Southwood, 1977) and the subsequent functional trait research program (McGill et al., 2006). The trait–based approach has the potential to increase drastically the predictive abilities of ecology in general. In field ecotoxicology, a counterpart of this approach has already been developed to detect and quantify the effects of contamination with pesticides at large spatial scales (Liess et al., 2008; Beketov et al., 2009; also see Section 4.1 for trait-based methods). All these conceptual advances, as well as many others, provide a theoretical background for understanding the effects of contaminants at broad spatial scales and in the presence of other factors.

5. Summary

The failure of the bottom-up approach in solving the central questions in ecotoxicology (see Section 1) and the success of the top-down approach in investigating and predicting large-scale ecological patterns in macroecology (see Section 2) reach us that
to understand large-scale ecological systems, which are characterised by complexity and variability, a combination of bottom-up and top-down research approaches is required. It is clear that, in ecotoxicology, the currently prevailing bottom-up paradigm requires the top-down one, and that neither of these two approaches can be successful in isolation from the other. To tackle the current pressing challenges, ecotoxicology has to progress using both approaches, similar to digging a tunnel from both ends at once.

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