Predictor sets and biodiversity assessment: the evolution and application of an idea

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The idea of “indicator species” is a relatively old one with a huge associated literature. The idea that the existence or health of a single species somehow captures the state of an entire ecosystem, though, remains a challenge to those who, like us, study entire assemblages of invertebrates. This challenge is especially marked when the ecosystems of choice are rainforests. Nevertheless there remains a need for a measure of diversity somewhere between the single species and the entire assemblage, which, for invertebrates in rainforests, may add up to many hundreds of species. This need led one of us (RK), in the nineteen nineties, to formulate the idea of a ‘predictor set’: that is, a statistically defined set of species, from within a much larger assemblage, whose spatial or temporal distribution captures the patterns characteristic of the entire assemblage.

This essay will trace the origin and development of this idea and present some current applications and future research questions. Of course, the use of single charismatic species as “flagship” or “umbrella” species is undoubtedly of conservation value and remains unchallenged.

Key words: Predictor set, indicator species, flagship species, rainforest, moths

THE GENESIS OF AN IDEA

FOLLOWING Kitching’s participation in the Royal Entomological Society’s centenary expedition to Sulawesi in 1985 (Knight and Holloway 1990) in which he assisted in canopy sampling using fogging techniques (a project led by Nigel Stork and Peter Hammond from the Natural History Museum, London), work began on assessing the arthropod faunas of Australian rainforest canopies using pyrethrum knock down techniques (see Kitching \textit{et al.} 1993). This project continued for many years and two things became apparent very rapidly: first, that species diversity in Australia’s rainforest canopies was very high and, second, that from an ecological viewpoint it was best approached using a comparative method rather than pursuing the unachievable goal of complete inventory.

The first of these outcomes was in no way surprising: early work by Erwin in Panama (Erwin 1982, Erwin and Scott 1980) and Stork and others in Borneo and Sulawesi (Stork 1987a, 1987b, Hammond 1990) had pioneered such canopy studies and shown extraordinary levels of diversity and novelty among canopy arthropods. Indeed it was Erwin’s work which led to the (in-)famous suggestion that we shared the planet with as many as 30 million arthropod species. This last figure is now more generally supposed to be between 3 and 8 million but the debate is on-going (Novotny \textit{et al.} 2007, Ødegaard 2000, Stork \textit{et al.} 2008, Hamilton \textit{et al.} 2010, Basset \textit{et al.} 2012).

The second early conclusion is a little more subtle and, indeed, led directly to the predictor set idea. It was apparent from the start that any attempt at assessing the alpha diversity of even a small patch of forest was hugely challenging. The vicissitudes of sampling, the varied biologies of the canopy fauna, and the short timeframe of most research projects meant that making statements about the complete diversity of the canopy was difficult. There are of course many statistically based extrapolation methods which do attempt this (see, e.g., Colwell and Coddington, 1994) and these are widely used. An alternative approach and the one we adopted later was a purely comparative one where we applied a mixed sampling programme to a particular patch of canopy (or entire forest) in a standard fashion (Kitching \textit{et al.} 2001, 2004). Then, assuming a baseline efficiency in the sampling programme, differences across sites could be analyzed and interpreted ecologically. In other words, measures of beta diversity could be made even where estimates of alpha diversity were (and were likely to remain) elusive (see, e.g., Kitching \textit{et al.} 1993, 2001, 2005).

There still remained the ‘problem’ of the sheer diversity of the rainforest samples, exacerbated especially when ‘shorthand’ versions of the results had the potential to be used in management applications. For this we need simpler, yet not simplistic, measures of diversity which can be used as surrogates for the unknown, perhaps unknowable, total diversity of the ecosystems we are studying.

The general idea of ‘indicator species’ of course had been around for many years. Fundamentally the idea was that the responses — ecological, behavioural or physiological – of a single species could act as a surrogate for those of a much larger set of species (ideally the entire ecological community). These ideas
appeared initially in the freshwater literature as biological responses to environmental degradation of water bodies were codified. The idea was later adapted in conservation management especially as the “species-centric” model of diversity management evolved. Resources became available for the study of selected iconic species, driven by national and international legislation which listed particular, usually vertebrate or plant species as being rare, vulnerable or endangered (e.g., Lindenmayer et al. 2000, Noss 1990, Shrivastava 2007).

For one studying the vast diversity of rainforest invertebrates the idea of selecting one species above all and assuming its responses to environmental change would be somehow characteristic of an entire assemblage rang false. We needed to identify a subset of the entire community for monitoring responses against whatever dimension of environmental change we were interested in but this could not be boiled down to one species — however rare, endangered or “iconic”. Far better to pick on a limited set of species which captured a more varied set of biological responses to environmental change. This would form a “predictor set” which might be targeted in future monitoring of responses to change. This general idea was presented and (obscurely) published in 1993 in a Workshop Proceedings volume (Kitching 1993a).

The review of McGeoch (1998) discusses at length many of the issues associated with using insects as indicators and should certainly be read in conjunction with this essay. In particular she stresses the similarities and differences among environmental, ecological and biodiversity indicators. Our “predictor sets” fit into her schema as both ecological and biodiversity indicators. As will become clear through our examples, we use predictor sets to characterise changes across particular ecological gradients (see the forest fragments and elevational gradient examples, below), but also to act as a statistical surrogate for the entire (or at least a much larger fraction of) biodiversity of a patch of forest (see our second example on changes along a latitudinal gradient).

This was clearly an idea whose time had come and others lit on the same notion, if not exactly the same nomenclature (Kremen et al. 1993; Didham et al. 1996). The term fell on fertile ground and the idea rapidly made its way into a wider literature (Gaston and Spicer, 1998, Cranston and Hillman 2002, Lewis and Basset 2007, Basset et al. 2008).

An ideal predictor set needs to have several qualities, viz.:

- It must be a set of taxa (species, morphospecies, genera, families etc) whose statistical distribution within a much wider assemblage of taxa has the same (or clearer) relationships with the environmental variable(s) under study as does the entire assemblage.
- The choice of taxa within the predictor set should be pre-defined in a quantifiable way.
- The set of taxa should contain, wherever possible, a range of functional groups to capture the biological variety of the assemblage as a whole.
- The members of the predictor set should be readily sampled and identifiable.

Needless to say this set of criteria is difficult to meet in every case but as a shopping list of “desirables” it remains useful.

By way of example we present Figure 1. Figure 1a is a multi-dimensional scaling ordination of a large sample of moths collected along an altitudinal gradient in sub-tropical rainforest in Yunnan in south-west China. The ecological details and justification will appear elsewhere: here we present it as part of an example of a ‘statistically defined’ predictor set. The pattern described in the figure is based on an analysis of the total of 1438 species of moths.

![Fig. 1. Ordinations of moth assemblages along a 1000m elevational gradient from Ailoa Shan, Yunnan, China: (a) based on the entire sample and (b) using only those species of restricted elevational ranges (see text).](image-url)
encountered in our survey. There is a clear, highly significant pattern (Pseudo-F = 5.8, p > 0.001) implying that there are clear differences in the occurrence and relative abundance of moth species associated with different elevations. Figure 1b is discussed below.

To generate useful tools for monitoring future change in these distributions (such as associated shifts in distributions due to global warming, for example), a management agency would have difficulty sampling, recognizing and analyzing the entire target fauna of 1400 species. Accordingly we selected from the larger data set those species which were common and had restricted elevational distributions. A total of 147 species fitted this prescription. Re-doing the ordination using just these species produces Figure 1b. Inevitably, this shows an even tighter set of groupings defined by elevation (Pseudo-F = 21.5, p < 0.001). Indeed the two figures (1a and 1b) are in no sense independent of each other but the second is based on a subset of the information contained in the first. Yet we have now used strict statistically defined protocols to identify a (relatively) small subset of species which capture the “behaviour” of the much larger, more intractable, group: we have defined a “predictor set”. The target set could be reduced even further by imposing further “entry requirements” on the subset (see below).

Once the general (and fairly obvious) idea of a predictor set was clearly stated it became one of the central tasks of our research group to develop studies in which the concept was put to the test. We present here three of these studies, each of which shows up some of the strengths and weaknesses of the idea and its application.

APPLICATIONS AND DEVELOPMENT OF AN IDEA

Moths in a Fragmented Landscape

The Atherton Tablelands of far northern Queensland present a fragmented landscape: abandoned dairy pastures alternate with arable lands and dotted among these are the remnants of the tropical rainforests which, until the early 20th Century covered these lands in dense forest. We selected nine such remnants, three of which had never been cleared — just isolated, three were about 40-60 year naturally regrown forests, and three were “scramblerlands” cleared within two years of our studies. We used simple light traps to sample the moth fauna within each of these on two occasions — during the northern dry and wet seasons, respectively. The results have been comprehensively published in Orr and Kitching (1999, 2003) and Kitching et al (2000).

In summary, we sampled 15,632 moths of 835 species. We sorted these to morphospecies and then grouped these into families or, in the case of the huge families which are a commonplace within the Lepidoptera, subfamilies. We analysed these using a different form of multivariate analysis: a modified principal components analysis (Thalib and Kitching, 1999). This allowed us not only to show clearly that there were different sets of taxa associated with the different classes of remnant, but also to identify which particular taxa contributed to these patterns and by how much. By adopting a stopping rule along the lines of “we will not consider any a taxon which contributes less than (say) 10% to the overall pattern strength”, we were able to identify a predictor set at the level of the family/subfamily. These analyses showed that nine families or subfamilies out of the 60 represented in our samples (Orr and Kitching, 1999) were strongly associated with the more disturbed sites, seven with the less disturbed remnants.

Of the first set (the “more disturbed specialists”) all but one of the nine taxa belong in the superfamilies Noctuoidea (as currently defined). The seven taxa associated with less disturbed sites included four subfamilies of the Geometridae, plus one subfamily of Noctuoidea (then designated the family Lymantriidae), one of the family Pyralidae, and the small family Anthelidae. These taxa were the overall predictor set for monitoring the environmental quality of rainforest remnants at least on the Atherton Tablelands. Using the weighted sum of these higher taxa captured the state of disturbance of the forest patches with considerable accuracy. A robust “first-pass” index of the state of disturbance of these forest remnants was provided by the simple ratio of the number of individuals of the Noctuoidea to those of the Geometridae (both relatively easily recognised groups). As a likely simple explanation we noted that the larvae of most noctuoids feed on grasses and other monocotyledonous plants, whereas those of geometrids on woody plants, creepers and vines.

This study clarified several issues pertinent to the general predictor set approach. First it is essential to have a comprehensive baseline survey of the target taxa before putative members of the predictor set can be proposed. Identification of the predictor set is definitely an "a posteriori" process! This then raises the thorny issue of just how widely can the outcomes of a particular study be applied? In the case of our Atherton Tablelands work the clear applicability is to forest fragments between 17° and 18°S at about 600 and 750 m asl, located on a granite basement rock. Strictly speaking application to other remnants at different latitudes, elevations...
or rock types is questionable. Obviously, an extensive and relatively expensive study cannot be carried out in every location which we may wish subsequently to monitor. In the absence of an extensive set of comparative studies we can only fall back on “professional judgement” when deciding to apply research outcomes in unresearched locations.

Insect Orders along a Latitudinal Gradient

We made a separate and different test of the predictor set idea over the period 2000 to 2007. During that period we established a set of one-hectare reference plots in rainforests from Lamington National Park in south-east Queensland to Cat Tien National Park in southern Vietnam. Ultimately there were 11 of these plots, seven in Australia (at Lamington, the Conondales, Eungella, Paluma, the Atherton Tablelands and Cape Tribulation), two in Papua New Guinea, one in Brunei and the aforementioned site in Vietnam. At each site a standard survey protocol was applied. All trees above 5 cm diameter at 1.4 m were mapped, measured and identified. In addition up to eight different insect trapping methods were applied in a standard manner (canopy fogging, pitfalls, litter extractions, interception traps, Malaise traps, yellow pan (“water”) traps, bark spraying and light traps). All catches were sorted to order (except for light traps from which the catches were sorted to morphospecies).

The overall protocol is described in Kitching et al. (2005). Vegetation results are variously presented in Laidlaw (1999), Laidlaw et al. (2000, 2007) and Small et al. (2004). Results on the insect surveys can be found in Kitching (2001), Kitching et al. (2004) and Majer et al. (2001).

In Kitching et al. (2001) we tackled the difficult question of which taxa and which trapping methods were most effective for a rapid biodiversity assessment. In other words we now sought a predictor set in terms of target taxa and the most efficient means of sampling them. We based our conclusions on a detailed analysis of the outcomes from four of our one hectare surveys: those from Lamington National Park, Eungella, the Atherton Tablelands and Kuala Belalong, Brunei. Overall samples containing 63,714 arthropods were analyzed resulting from seven trapping methods. No light trap catches were included.

Using data from each of the four locations, we searched for significant differences in catches across insect orders and methods then totalled formally significant outcomes in each case. In a matrix of seven trapping methods by 11 arthropod taxa, 31 significant ($p<0.05$) outcomes were obtained. Three trapping methods showed significant results across six or more taxa. No other trapping method scored more than four “significant” taxa. Three taxa showed significant patterns across four or more trapping techniques. No other taxon scored more than three “significant” trapping methods. The most effective trapping methods were canopy fogging, bark sprays and litter extractions (see Kitching et al. 2005 for technical details). Turning these results into a ‘rapid’ protocol in which site to site discrimination was likely to be identified with a minimum of trapping and sorting effort we were able to recommend that Collembola, Hemiptera and Hymenoptera: Formicidae (ants) should be targeted using a combination of bark spraying, canopy fogging and litter extractions.

This study again showed up interesting strengths and weaknesses. Its strengths were that clear discrimination was possible based on just three readily identifiable taxa at a very high taxonomic level. This was underlined by the general ecological differences between the groups — decomposers (most Collembola), herbivores (most Hemiptera) and predators (most ants). Its weaknesses included the fact that one of the recommended sampling methods — canopy pyrethrum knockdown — is technically challenging. In addition sorting animals to higher taxonomic resolution may conceal nuances of ecology and natural history which may be interesting and, even, useful in development of more focussed monitoring efforts. The issues associated with the extrapolation of results beyond the four sites analysed, highlighted already in the previous example, remain in this example also.

Moths along an Elevational Gradient

The final case history we present is the most recent. From 2006 until 2010 we participated in the IBISCA-Queensland project (Kitching et al. 2011). This was a multi-taxon, multi-scientist international collaboration which brought a total of 55 scientists from 14 countries to south-east Queensland to examine the ways in which animal and plant diversity changed over a set of twenty fixed plots arranged in sets of four, at 300 m, 500 m, 700 m, 900 m and 1 100 m above sea-level. The general model for large-scale studies of arthropod diversity using a fixed experimental design, and then inviting many different specialists to run subprojects within the general design constraints, was developed earlier in Panama (Basset et al. 2007). The IBISCA-Panama project investigated canopy/ground contrasts in arthropod diversity. Later “IBISCA” (Investigating the Biodiversity of Soil and Canopy Arthropods) projects have focussed on quantifying different dimensions of arthropod diversity change in Vanuatu, France and, most recently, Papua New Guinea.
The general rationale for the IBISCA-Queensland project was that elevational change, within a continuous block of forest (in this case rainforests within the 23,000 ha of Lamington National Park), could act as an adequate surrogate for changes in climate. Each 200 m change in elevation represents about a 1.5°C change in average temperature. By examining the ways in which different taxa changed we hoped to gain insights into how faunas might change with predicted changing climate and, more important in the present context, identify predictor sets which could be used to monitor such changes in the future.

We analysed data from many taxa including moths, ants, beetles, flies, thrips and vascular plants. A summary of several of these results is in Kitching et al. 2013 and extensive descriptive results are in a Special Issue of the Memoirs of the Queensland Museum (Burwell et al. 2011). Our primary focus, again, was on moths sampled using light traps (Ashton et al. 2011). Our analysis began by an exploration of the data using a multi-dimensional scaling ordination.

There was a clear differentiation among the all taxon-specific assemblages from each elevation and each season that was sampled. For the assemblage of moths we were able to pick out a set of 28 species which fulfilled a number of criteria, viz.:

- Species were represented in our samples by at least 30 individuals
- At least 80% of individuals encountered were restricted to one or a small contiguous range of elevations.

We were able to identify 18 of these 28 taxa, confidently, to species. These 18 species (of the total of 865 species encountered in the study) best captured the elevation to elevation changes. Nine were restricted to a single elevation, six species were spread over two adjacent elevations, and a further three species had wider but contiguous spreads.

It was the stated aim of the IBISCA project to develop, among other things, a set of target species which could be used by managers as monitors of future change. Clearly these 18 moth species are candidates for inclusion in such a predictor set (and similar lists of other taxa have also been identified). Using the moths as an example, we now ask the question, is this the best set of species to recommend for management use? To tackle this question realistically we need to define properties of those who would be doing the monitoring. They are likely to have the following characteristics:

- They will not be experienced moth specialists
- They will have minimal time (and, probably, financial) resources available for sorting.

Fig. 2. The ‘predictor set’ of moths derived from the IBISCA Queensland study described in the text. Species 1 – Termessa gratiosa (Walker), 2 – Lycene stricta (Walker), 3 – Asura cervicallis (Walker), 4 – Palaeosa bicosta (Walker), 5 – Xylophonus leptomiola (Turner), 6 – Laophylla ammata Turner, 7 – Lychnographa heroica Turner, 8 – Heterochaeta conglobata (Walker), 9 – Middletonia hemichroma (Turner). Figure courtesy of Mr Geoff Thompson, Queensland Museum.
This suggests that subtle differences in shade and pattern (which separate many moth species from each other) are likely to be overlooked. Re-examining the set of species in this light it is straightforward to pick out nine which are clearly marked, shaped and/or coloured and need little experience for their recognition. These are illustrated in Figure 2. This subset of species also have ranges that vary from lowland restricted to upland restricted with various intermediate ranges. This set we propose as our “monitoring-friendly” predictor set.

The whole IBISCA Queensland Project was predicated upon the idea that we need to identify predictor sets to monitor future climate change. It was no part of our project to do the actual monitoring. Indeed, from the point of view of monitoring climate change this would involve a minimum twenty year project.

This does raise an important general issue with our predictor set concept. Across our several projects our research has had two major goals. The first has been to identify patterns in diversity across different dimensions of environmental change (remnant quality, latitudinal contrasts, adjacent climates) and at least hypothesize what underlying ecological and biogeographical mechanisms may produce these patterns. In this regard the research outcomes are under the control of our co-workers and ourselves. The second goal though has been to produce monitoring tools which may be used by others: either other scientists or managers charged with monitoring. Of these two constituencies we have had more success with the first than the second.

Three sets of projects have adopted at least some of our methodologies (although not, explicitly, our predictor sets of taxa). The first of these has been the regional biodiversity assessments promoted by the Diversitas Western Pacific and Asia programme (see Nakashizuka and Stork, 2002). Elements of our plot assessment protocols were also incorporated in the insect assessment projects of both the Centre for Tropical Forest Research (CTFS)(see http://www.ctfs.si.edu/group/arthropod%20monitoring/) and the four IBISCA projects in Panama, Queensland, Vanuatu and France (see above and Basset et al. 2007, Tardieu and Barneoud 2008, Kitching et al. 2011).

The uptake of these and similar results by managers is more problematical (as with many outcomes of applied ecological work). There are many reasons for this. On the one hand the widespread “downsizing” of many management agencies and their reliance on outsourcing has reduced the availability of both time and scientific capacity within agencies. Some comment though can be made. At least one of our projects (the Atherton fragmentation study) was funded by a management agency (the Wet Tropics Management Authority). Why then were the very clear results not taken up?

We can only speculate about the reasons. Three issues may be involved:

(a) the will and funding for long-term monitoring was simply not there: this is in spite of its prominence in general management rhetoric;

(b) diverting attention to non-charismatic and unfamiliar taxa such as the arthropods was perhaps ineffective in competition with tree kangaroos, cassowaries and crocodiles; and,

(c) the particular “champion” for arthropod monitoring within the administration transferred to another position.

Issues such as these may be largely beyond any influence of the researchers themselves. We do, however, have capacity to make our results more accessible to our user communities. In this regard the many volumes of syntheses about conservation science and policy published and promoted by Ivor Beatty have been fine examples.

**THE FUTURE OF AN IDEA**

We have demonstrated, to our satisfaction, that the predictor set idea is useful and can be supported by field results. Three areas though demand further attention and, indeed, are part of our current research programme.

1. **Formalizing the species-choice procedure**

We have, hereto used pragmatic and *ad hoc* criteria for deciding which species should be included or excluded from a predictor set. A more formal and uniform approach is desirable. Several alternatives are available. In other work we have used the generally applicable IndVal procedure of Dufresne and Legendre (1997) (see also Podani and Csanyi 2010) to identify the basic species list from which a more subjective predictor set can be chosen. This approach combines considerations of specificity (restriction to particular site types) with fidelity (the likelihood of occurrence of a species within a particular site type).

2. **Calculating the significance level of the predictor set**

Like all areas of ecology the identification of a predictor set is probabilistic and even when a standard numerical procedure like the IndVal approach is use there is still the possibility of making Type 2 errors where species appear as “significant” indicators by chance. Modern simulation methods based on random resampling...
of diversity data-sets allow probabilities to be attached to particular outcomes of the IndVal analysis. The development and evaluation of this approach is part of our current research programme.

3. Validating the predictor set

Finally, whenever a predictor set is identified by whatever methodology, the need for validation is obvious. The “traditional” way to validate a scientific result is to compare outputs from analysis of a particular data set with a parallel but independently collected data set. This may be problematical when dealing with extensive biodiversity data-sets as replication is often logistically impossible (different times, seasons, exact locations etc) and likely to be expensive. We do have the opportunity to test at least one set of outcomes from our research. The transect established in subtropical rainforest in Lamington National Park (see above) has been matched by one just a few kilometres to the south in the Border Ranges National Park, New South Wales. Both transects are in subtropical forest ranging from notophyll vine forest about 300 m asl to microphyll fern forest (cool temperate rainforest) at above 1000 m asl. The transects have different aspects (SW compared with NW) and the NSW site has been lightly logged over 40 years ago. Nevertheless, the sites are similar and comparable. We have surveyed plants and moths on both these transects and are in process of evaluating the results in the second (Border Ranges) transect against those obtained in the Lamington locations. This comparison, when complete, will provide a validation of the predictor set identified from Lamington.

Other validation work in progress within our group involves taking some of the very rich data sets we have from sites in Australia and China, dividing them in half randomly, and comparing the predictor sets obtained independently for each half of the sample.

CONCLUSION

We faced a daunting task when confronted with the rich arthropod faunas of Australian rainforests. Not only were the numbers of species in the thousands but, depending on the taxon investigated, these species were often unnamed. To cope with this potentially overwhelming journey we learned to sort mixed samples into higher taxa (Orders, Families) and subsequently into ‘morpho’-species. Even then the sheer numbers of taxonomic units was challenging. Picking out subsets that reflected the underlying ecological patterns of the larger assemblages led to the predictor set idea, which is proving robust and useful.

DEDICATION

This essay is respectfully dedicated to the late Mr Ivor Beatty who, through his support for local science publishing, did so much to encourage Australian scientists. Ivor distributed Insect Ecology 2nd Edn (Matthews and Kitching, 1984), and published The Ecology of Australia’s Wet Tropics (Kitching, ed., 1988) and, most recently, Remnants of Gondwana (Kitching, Braithwaite and Cavanaugh, eds, 2010). We are and will remain grateful to him for the opportunities he created for so many.

REFERENCES


