

# Improving the application of vertebrate trait-based frameworks to the study of ecosystem services

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## Summary

1. Examining the consequences of environmental change for the provision of ecosystem services can be facilitated through trait-based frameworks that consider linkages between traits that influence a species' response to change and traits that determine its effect on ecosystem services.
2. Developing these frameworks requires a systematic approach to trait selection and addressing the interrelationships among the scale of the environmental change, area of ecosystem service provision and the most appropriate traits for analysis.
3. We examine key issues in the application of trait approaches to vertebrates, drawing specifically on the substantial progress made in this area for plants. We argue that vertebrate ecologists need to develop more coherent and systematic trait-based approaches that are broadly applicable.
4. We present a new framework for selecting response and effect traits to link environmental change with ecosystem services. An empirical example of each step in the framework is provided using birds as a case study, linking the environmental change of loss of tree cover with the ecosystem service of invertebrate pest regulation in apple orchards. We found that as tree cover around orchards increased so did the abundance and foraging rate of bird species that pursue invertebrates in flight, and this may help reduce the abundance of certain pests of apples (e.g. adult stages of *Cydia pomonella* and *Helicoverpa armigera*).
5. Implementing a systematic and transparent approach to trait selection should further refine the development of trait-based approaches for vertebrates.

**Key-words:** avian function, birds, ecosystem function, effect traits, environmental change, functional traits, response traits, trait approaches

## Introduction

There is growing recognition that functional diversity rather than species diversity *per se* is more important in maintaining an array of ecosystem functions (Díaz & Cabido 2001; Flynn *et al.* 2009). To examine the consequences of environmental change for ecosystem functioning through changes in functional diversity (i.e. the range of functional trait values present in a community), researchers must identify species traits that can dictate how species respond to change and traits that determine their effect on function (Díaz & Cabido 2001). The use of trait-based frameworks has assisted the study of the interrelationships among environmental change, functional diversity and ecosystem function (Díaz *et al.* 2007). These frameworks have enormous potential to improve broad-scale management of ecosystem services (i.e. ecosystem functions that benefit humans) and avoid service

disruption through environmental perturbations that alter trait assemblages. However, current trait-based approaches in this area have developed almost exclusively through work on plants. Little attention has been given to their application at higher trophic levels or to other taxonomic groups (but see de Bello *et al.* 2010).

In animal ecology, classifying species into groups based on similar ecological characteristics (*c.* traits) has a long history. For example, Salt (1953) and Root (1967) assigned different bird species to groups based on similar foraging behaviour; the latter author being credited as the first to introduce the concept of an 'ecological guild' (Simberloff & Dayan 1991), which was defined as '...a group of species that exploit the same class of environmental resources in a similar way.' (Root 1967, p. 335). The guild concept has been used widely, particularly in avian ecology (e.g. Noon 1981; Verner 1984; Szaro 1986; Rogers & Smith 1993; Rodríguez, Jansson & Andrén 2007). Bird guilds are often defined based on similarities in foraging behaviour among species, which implicitly

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recognises the importance of species traits in influencing ecosystem function (see Defining effect traits). Some authors have also defined 'response guilds' (e.g. Szaro 1986; Rogers & Smith 1993) where species with similar ecological characteristics are predicted to exhibit similar responses to environmental change (see Defining response traits).

In addition to the guild concept, trait-based approaches have been applied more explicitly in animal studies primarily to predict species' responses to environmental change (e.g. Hausner, Yoccoz & Ims 2003; Öckinger *et al.* 2010; Azeria *et al.* 2011; Langlands *et al.* 2011). Yet, methodological development of trait approaches in fauna ecology substantially lags behind the advances made in plant ecology in the last two decades. These advances include establishing standardised methods for selecting and measuring plant traits (McIntyre *et al.* 1999; Cornelissen *et al.* 2003) and developing frameworks that aim to predict the consequences of environmental change for ecosystem function through linking plant response and effect traits (Díaz *et al.* 2007; Fortunel *et al.* 2009).

We have three primary aims. First, we discuss the key issues that need to be addressed to improve the application of trait-based approaches in animal ecology. Second, we present a comprehensive and systematic framework to guide trait selection in fauna studies. This framework describes a process for justifying trait selection across different contexts and aims to avoid the proliferation of ad hoc lists of traits used in analyses. While expert opinion will always be important in trait selection, it is crucial for experts and nonexperts to follow a transparent and systematic process to selecting traits to allow others to replicate the approach and assess the justification for each decision. Finally, we illustrate empirically the application of our trait-selection framework and demonstrate a method for linking response and effect traits in birds to examine the consequences of environmental change for the provision of ecosystem services. The latter is timely given the increasing recognition of the importance of animals in providing ecosystem services such as pollination and biological control (see Luck *et al.* 2009).

Our emphasis is on improving vertebrate trait-based frameworks, although many of the issues we discuss are relevant also to invertebrates, where similar approaches are applied (e.g. Barton *et al.* 2011; Diamond *et al.* 2011). In our trait-selection framework, we focus primarily on what Fisher, Turner & Morling (2009) describe as 'intermediate services'. These are ecological functions that support human well-being (e.g. pollination of food crops), which we label simply as ecosystem services.

### Key issues in improving vertebrate trait-based frameworks

Definitions of 'trait' vary throughout the literature. Traits are usually defined at the level of the individual, but the concept has been applied at various levels of organisation (e.g. population or community; Violle *et al.* 2007). Violle *et al.* (2007; p. 884) defined a plant trait as '...any morphological,

physiological or phenological feature measurable at the individual level, from the cell to the whole-organism level, without reference to the environment or any other level of organisation.' Here, we emphasise morphological, physiological and life-history (*c.* behavioural) features of fauna that can be measured at the individual level. However, some life-history traits (e.g. habitat use) can only be measured with reference to the surrounding environment. We prefer to retain these traits owing to their importance in understanding the implications of environmental change for ecosystem services. We acknowledge also that population or species-level characteristics such as population growth rate or geographic distribution are vital to this understanding, but focus on individual-level traits in line with much of the literature.

### DEFINING RESPONSE TRAITS

Response traits dictate the response of organisms to environmental change (Lavorel & Garnier 2002), but this idea has been differently applied. In some cases, a response trait is measured as a change in the attribute (the quantitative value) of a trait for a given species across an environmental gradient. This could be defined as a 'direct response trait' whereby the trait(s) of a particular species changes in response to environmental variation (e.g. through adaptation). For example, Alexander *et al.* (2009) examined changes in the growth and reproductive traits (e.g. number of inflorescences and seed size) of Asteraceae forbs along altitudinal gradients. This study documented intraspecific variability in the characteristics of individuals that occupied the entire gradient.

However, the concept is also applied to describe characteristics of organisms that may result in changes to, for example, their population size with environmental change. Here, a trait could be defined as a 'response-mediating trait'. For example, Davies *et al.* (2010) examined relationships between species traits (e.g. foraging behaviour) and population change in arid-zone birds in response to changes in water availability and livestock grazing. Other fauna studies correlate traits (e.g. body size) with extinction risk to identify the types of species most susceptible to extinction from particular disturbances (e.g. Cardillo *et al.* 2008; Fritz, Bininda-Emonds & Purvis 2009). It is important to note that a given trait may be both a direct response trait and a response-mediating trait.

Measuring change in species abundance as a response to environmental perturbations was common in early plant studies that sought to identify, for example, 'increaser', 'decreaser' and 'neutral' species (Dyksterhuis 1946). The evolution to quantitative analyses of variability in plant traits was facilitated greatly through the development of well-established trait lists and methods (Weiher *et al.* 1999). We argue that trait-based approaches applied to fauna would benefit substantially from a similar evolution in consideration of appropriate trait lists and systematic methods for trait selection and analysis. Direct response traits and response-mediating traits are both relevant to assessing the implications of biotic responses to environmental change for

ecosystem service provision, because the contribution of species to services is dictated by intra- and interspecific trait variation and change in abundance (Garnier *et al.* 2007). In our study, we focus on response-mediating traits (hereafter: 'response traits').

#### DEFINING EFFECT TRAITS

Effect traits determine the effect an organism has on ecosystem functioning (Lavorel & Garnier 2002), and current effect-trait frameworks are dominated by studies on plants. While much of this research has focussed on the relationships between functional diversity (e.g. the number of functional groups) and its importance in supporting particular functions or ecosystem services (Balvanera *et al.* 2006), species traits are key to understanding how particular species affect ecosystem function (Hooper *et al.* 2005). For example, the effect traits of flower height preference, daily time of flower visitation and within-flower behaviour in bee pollinators acted in a complementary fashion to improve seed set in pumpkin crops (Hoehn *et al.* 2008). Mokany, Ash & Roxburgh (2008) found that the effect traits of the most dominant plant species in native grassland communities had a greater influence on a number of ecosystem functions (e.g. water use and light interception) than overall functional diversity.

In plant-based research, the ecosystem function of interest is occasionally an aggregate characteristic of the species delivering the function. For example, experimental studies have examined how species/functional diversity or plant traits influence the function of biomass production whereby 'biomass' is measured from those plants providing the function (Wardle, Bonner & Barker 2000). This is fundamentally different to most vertebrate-based studies where the function usually represents an intertrophic effect (e.g. pollination of plants or dispersal of seeds). In both cases, careful consideration of the trait-selection process is vital to ensure the most appropriate effect traits are chosen that are clearly linked to the particular ecosystem function or service and the measure of its delivery (e.g. pollen deposition).

#### LINKING RESPONSE AND EFFECT TRAITS

Linking response and effect traits can theoretically be used to predict how environmental change may impact on the provision of ecosystem services, and conceptual frameworks to promote this idea have been developed using primary producers (Suding & Goldstein 2008; Fortunel *et al.* 2009) and across trophic levels (Lavorel *et al.* 2009). There are also a handful of empirical examples. De Deyn, Cornelissen & Bardgett (2008) demonstrated how plant responses to extreme temperatures and low nutrient availability had major implications for carbon cycling through the interplay between response and effect traits. Spooner & Vaughn (2008) found that the response of mussel species to changes in water temperature impacted on their contribution to ecosystem services such as nutrient excretion and benthic–pelagic coupling.

Ability to predict the implications of environmental change for ecosystem services is substantially enhanced when the same traits (e.g. leaf area) or correlated traits dictate both species responses to a changing environment and their effects on service provision (Lavorel & Garnier 2002; Suding *et al.* 2008). There is some evidence that this is true for plants (Suding & Goldstein 2008), and it may be true for vertebrates, although the idea has not been comprehensively tested. For example, in frugivorous birds, the capacity to move between spatially discrete habitat patches can determine a species' response to declining landscape connectivity and its contribution to forest maintenance through seed dispersal. 'Body size' is another vertebrate trait that can relate strongly to a species' contribution to ecosystem function and susceptibility to environmental threats. Jordano *et al.* (2007) found that large mammals were important for long-distance seed-dispersal events, while mammal body size can also be positively correlated to a species' susceptibility to habitat disturbance (although this varies across regions; Fritz, Bininda-Emonds & Purvis 2009).

#### LEVEL OF TRAIT VARIATION

Morphology, physiology, phenology and behaviour vary in space and time within species, and this will affect the trait attributes they exhibit in different contexts whether as genotypic turnover or plasticity (Naeem & Wright 2003). Farias & Jaksic (2009) assessed the relative contribution of species turnover and phenotypic plasticity to measures of functional diversity using changes in predator diets across 17 years and found that the latter had a strong influence on interpreting the functional dynamics of the community. Conversely, some trait attributes do not vary greatly across species, constrained by, for example, evolutionary history. In Australian birds, clutch size varies little among many of the old endemic species (Yom-Tov 1987) and this would not be a suitable trait to use to identify which of these species may decline in response to environmental change.

Spatio-temporal variation in the trait attributes of individuals from the same species increases the uncertainty surrounding predictions about a species' response and effect. Researchers must consider the degree of variability likely to occur in trait attributes (Violle *et al.* 2007). Spatio-temporal variability in trait attributes will influence a species' contribution to ecosystem services and their response to environmental change. Evidence of such variability could be obtained from research on species behaviour separated in time and space (e.g. across seasons and locations), although the contribution of methodological differences between studies to any observed variability must be considered.

#### SCALE OF ANALYSIS

Many experimental and field-based studies on plants that test biodiversity–ecosystem function relationships have been conducted at very small spatial scales (plots of m<sup>2</sup>; Balvanera *et al.* 2006). This may be appropriate when examining the

relationships between grasses and forbs and ecosystem functions such as biomass production, but such small scales of analysis are not appropriate for larger plant species or more mobile taxonomic groups (e.g. mammals and birds), or for studying ecological processes such as dispersal.

Linking environmental change with species response via response traits must consider the type and scale of the change and how this might interact with responses and influence selection of the most appropriate traits to measure. We argue that the environmental change of interest is the best starting point to address this issue and will dictate the selection of the most appropriate response traits. Consideration of the environmental change and appropriate response traits should guide selection of the best scale of analysis, in addition to the range of movement of the focal taxon or group. For example, Pöyry *et al.* (2009) examined range shifts in Finnish butterflies as a (possible) response to climate change as a factor of species traits such as mobility, body size and habitat use. They used a 10 km × 10 km grid as their scale (grain size) of observation with Finland as the extent. While other traits and spatial scales may be chosen to assess the response to this environmental change, some traits (e.g. mobility) are intuitively relevant and grain sizes of square kilometres seem more appropriate than square metres.

For analyses linking ecosystem services to effect traits, trait selection should be influenced by the interaction between the particular service, the area (scale) over which the service is provided (e.g. crop area) and the type of service delivery required (e.g. crop type). For example, pollination at the level of an individual farm or crop may depend more on traits related to morphology and daily movements, whereas pollination across many farms will rely on both these traits plus traits related to, for example, habitat use and dispersal behaviour. The service of interest and the type and area of its delivery should dictate trait selection and ultimately the measurement of trait attributes. A major challenge for trait-based studies therefore is selecting the most appropriate scale of measurement when considering the overlap between response and effect traits, particularly when attempting to identify traits that dictate both response to change and effect on services. In these cases, it may be desirable to select traits aligned with a nested hierarchy of scales most relevant to the response and effect of interest.

#### PHYLOGENY

Phylogeny can account for variation in trait attributes among species, at least for certain types of traits (e.g. morphological and life-history; Böhning-Gaese & Oberrath 1999; Freckleton, Harvey & Pagel 2002), and some studies account for phylogenetic relationships among species prior to identifying traits that confer greater susceptibility to extinction (e.g. Cardillo *et al.* 2008; Fritz, Bininda-Emonds & Purvis 2009). Species that are more closely related may exhibit similar responses to environmental perturbations independent of similarity in traits. Moreover, phylogenetic diversity may explain more variation in community-level parameters (e.g. plant biomass

production) than species or functional diversity *per se* (Cadotte, Cardinale & Oakley 2008). Addressing phylogenetic relatedness among species when examining environment–trait relationships is possible if phylogenetic trees for the focal taxonomic group (and region) are available (e.g. Poff *et al.* 2006; Willis *et al.* 2008). However, studies that establish the utility of taking phylogenetic relatedness into account in functional trait research may be needed to justify the extra effort this approach requires.

#### TRAIT SELECTION

While fundamentally important, trait selection is sometimes poorly dealt with by researchers, particularly for fauna studies. Agreement on a standardised approach is crucial because the results of functional analyses rest heavily on the selection of traits for inclusion (McIntyre *et al.* 1999; Weiher *et al.* 1999; Bernhardt-Römermann *et al.* 2008). For the most part, researchers select traits that are relevant to the environmental change of interest (for response traits) or the ecosystem function (for effect traits). Justification is usually based on ecological knowledge or evidence from the literature (e.g. Cavender-Bares, Kitajima & Bazzaz 2004; Alexander *et al.* 2009; Fritz, Bininda-Emonds & Purvis 2009). Occasionally, ease of measurement is used to justify trait selection (e.g. Dumay *et al.* 2004), but this is only appropriate when no other options are available (Lavorel & Garnier 2002). A worst-case scenario is when trait selection is not justified, implying ad hoc selection.

It is vital to take a systematic and ecologically defensible approach to trait selection that considers relevant responses and effects for the taxonomic group(s) being studied, and the most appropriate spatial scale for matching organism activity with the response/effect. For example, in birds, body size relates to, among other things, metabolic rate, foraging behaviour, longevity and territory size (Brown, Calder & Kodric-Brown 1978). Hence, examinations of the contribution of nectar-feeding birds to crop pollination would need to include the trait of body size, which is likely to be relevant at multiple spatial scales. The relationship between body size and daily energy requirements would dictate site-specific pollination contribution, while the relationship between body size and range of movement would determine the contribution of species to pollination across broader areas (e.g. whole crops, farms or landscapes). Conversely, bill morphology would also influence pollination contribution at local scales, but not be relevant to the contribution of species at larger scales as it has no relationship with range of movement (to the best of our knowledge).

### Materials and methods

#### OVERVIEW

We demonstrate an approach to selecting vertebrate traits to assess the consequences of environmental change for the provision of ecosystem services and present a structured set of stages for trait



selection illustrated with a particular data set. Birds are used as a case study because they fill a diverse range of ecological niches, contribute to many different ecosystem services, and are arguably the most extensively studied vertebrate group (Sekercioglu 2006a). However, our approach is broadly applicable and relevant to all fauna groups.

We illustrate a process rather than provide an exhaustive list of traits at any level of the selection framework or attempt an extensive justification of trait selection, although we acknowledge its importance. For the sake of simplicity, we focus on a single environmental change – tree loss, and a single ecosystem service – invertebrate pest regulation. We hypothesise that birds with certain traits will record a response to variation in tree cover through change in abundance across sites and this may have implications for pest regulation depending on the correspondence between response and effect traits.

#### SITE SELECTION AND BIRD SURVEYS

Previous studies have demonstrated the contribution of birds to controlling invertebrate pests in apple orchards, leading to an increase in crop yield for growers (Mols & Visser 2007). We collected data on bird species occurrence and abundance in 30 sites (each site was a 2-ha transect) across seven apple orchards in northern Victoria, Australia. Birds were surveyed using a line transect method and a distance sampling procedure (Buckland *et al.* 2001). Each site was surveyed for 20 min on four occasions during 2009 and 2010 at critical times of the crop growing season – flowering, early fruiting, late fruiting and post harvest. Surveys began at dawn and were completed by 10 am, and only birds using the orchard were included in sampling. Raw abundances were corrected for differences in detectability among species after calculating a detection probability using DISTANCE SAMPLING software (version 5.0; Thomas *et al.* 2010; see Appendix S1 in Supporting Information).

#### TRAIT DATA

The first step in the selection framework is to compile an extensive list of possible traits, which is later refined based on various criteria (see Results). We collected data on traits of bird species in our study area from extensive searches of the literature and primary sources (Table S1; Appendix S1 in Supporting Information). Sourcing trait information from the literature is most feasible for studies of highly mobile vertebrate communities across multiple sites, as it is extremely difficult to collect these data from direct measurements in the field.

#### ENVIRONMENTAL CHANGE

We measured differences in tree cover across sites based on a geographic information system database of land cover data from the Bureau of Rural Sciences (2002). Variation in tree cover was recorded for native vegetation and non-native vegetation such as plantations and treed horticulture, as both are likely to influence bird assemblages. We recorded the proportion of land covered in trees within a 5-km radius buffer around each bird survey site using ARCMAP 9.3.1 (ESRI 2009).

#### ECOSYSTEM SERVICE

To estimate the potential for birds to limit invertebrate populations, we collected data on bird foraging behaviour in each apple orchard for up to 3 h after completion of the line transects. While absolute foraging rate may be higher earlier in the morning, we were primarily interested in differences in relative foraging rate across orchards.

These data were then linked to the effect-trait data collected from the literature (see Results). We used a focal approach by selecting individual birds and recording their foraging locations (e.g. substrate and height), foraging manoeuvres and, if possible, food items consumed for up to 5 min for each individual. Foraging activity was converted to a foraging rate measured as the number of attempts to obtain food per minute. As invertebrates are a component of the diet of most of the species we recorded foraging in apple orchards, we calculated total foraging rate across all species (excluding rarely recorded species; Appendix S1 in Supporting Information) for each study site and used this as our measure of the potential capacity of birds to control invertebrate populations.

In Australia, the most damaging invertebrate pests in apple orchards include codling moth (*Cydia pomonella*), dimpling bug (*Campylomma liebknechti*), budworms (i.e. *Helicoverpa armigera* and *Helicoverpa punctigera*), fruit fly (i.e. *Bactrocera tryoni* and *Ceratitidis capitata*) and various species of inchworm (e.g. *Phrissogonus laticostata* and *Chloroclystis testulata*). These species will attack flowers, leaves and/or fruit throughout the growing season, and various life stages of these pests (e.g. larvae and adult) can be predated upon by birds.

Consistent with other community-level studies, our approach to recording foraging behaviour did not allow us to differentiate among the relative contribution of birds from different genders, age classes or reproductive status to pest regulation. Such detailed information is more commonly associated with studies of single species. Moreover, we could not identify individuals, but attempted to avoid collecting a large proportion of data on the same individuals by regularly moving to different locations within the orchard once foraging observations had been collected from a particular site.

Our data on foraging rate are only an estimate of the contribution of birds to pest regulation and are in lieu of quantitative data linking bird foraging behaviour with variation in invertebrate abundance and changes in crop yield or financial returns to growers. Such data were not available for our study, but could be obtained through, for example, controlled experiments that exclude certain bird species from apple trees (e.g. Mols & Visser 2007). While such experiments are difficult to replicate across multiple locations, they provide valuable detailed information that is hard to obtain in more generalised, broad-scale approaches such as the one we use here.

#### DATA ANALYSIS

We analysed the relationships between the potential response and effect traits and the environmental change (tree cover) and ecosystem service (invertebrate regulation), respectively, using RLQ analysis (Dolédec *et al.* 1996). RLQ is a multivariate approach that links information on species abundance, species traits and characteristics of the environment. It relies on the following three matrices: species  $\times$  site (i.e. species abundance at each site) from which is derived the 'L' table; species  $\times$  traits (i.e. trait values for each species) – the 'Q' table; and site  $\times$  environmental variable(s) (i.e. the value of each environmental parameter at each site) – the 'R' table. RLQ is an ordination method that links the three data matrices through, for example, a principal components analysis of the R and Q tables that is used to constrain a correspondence analysis of the L table. It identifies the strength of the association between species traits and the environment measures (see Dray, Chessel & Thioulouse 2003; Threlfall *et al.* 2011 for details).

We conducted the following two RLQ analyses: a response-trait analysis linking tree cover with bird species response traits through variation in bird species abundance across sites; and an effect-trait analysis linking foraging rate with bird species effect traits through

variation in bird species abundance. Our analysis determines whether certain traits are important in influencing the response of birds to changes in tree cover and subsequently total foraging rate in apple orchards (see Appendix S1 in Supporting Information). Analyses were conducted in R 2.13.1 (R Core Development Team 2011) using the package *ade4* (Dray & Dufour 2007). The overall significance of the relationship between species traits and tree cover, and species traits and foraging rate was assessed using a permutation test with 99 999 iterations. We did not consider phylogenetic relatedness in our analysis because phylogenetic trees for the bird species in our study region were not available.

## Results

### TRAIT-SELECTION FRAMEWORK

The first step in the trait-selection framework is to generate a list of potential traits, as extensive as possible based on current knowledge, which may be important in influencing the relationships between the target organisms and their environment (Pool 1; Fig. 1). To illustrate, we compiled an extensive list of avian traits that encompass morphology, physiology

and life-history (behavioural) aspects and categorised each as either a response (i.e. response-mediating trait) and/or effect trait (Table 1). The process could begin by listing traits relevant to the environmental change or ecosystem service of interest (i.e. begin at Pool 2), and the application of expert knowledge may be particularly crucial at this stage of the selection process. However, starting at Pool 2 requires the selection or rejection of traits from a larger pool known to the researcher, but not explicitly acknowledged. Presenting a more extensive list of traits up front greatly improves the transparency of the process and allows others to assess the logic applied to trait selection, as well as enhancing comparability of studies (McIntyre *et al.* 1999). Moreover, Pool 1 is extremely valuable when selecting traits relevant to other environmental perturbations or ecosystem services.

Decision Stage 1 (Fig. 1) requires selecting from the list of potential traits those relevant to the environmental change(s) and ecosystem service(s) of interest (Pool 2). This should be done for each individual change and service. Based on the evidence from the literature (see Table 1 for examples) and expert knowledge, we selected response traits most relevant to change in tree cover and effect traits most relevant to invertebrate pest regulation in apple orchards (Table 2). Here, we ask whether species with particular traits respond positively or negatively to loss of tree cover and what implications this has for invertebrate pest regulation in apple orchards viewed through species effect traits.

At Decision Stage 2, the list of possible response and effect traits will likely need to be narrowed based primarily on data availability (see Materials and methods), but also considering ease of measurement (if trait data are to be collected in the field), likely trait variation and correlations among traits (Pool 3). We cross-referenced our list of potential response and effect traits (Table 2) with a list of traits for which we were able to obtain data from extensive literature searches (Table S1 in Supporting Information) to produce a shorter list of traits with actual values (Table S2 in Supporting Information). We then reduced collinearity among trait values by removing certain traits (Appendix S1 in Supporting Information). The following traits were included for further analysis: response traits – body mass, habitat plasticity, vagility, nest type, nest location, foraging behaviour, foraging location, foraging location plasticity, foraging substrate, foraging substrate plasticity, diet and diet plasticity; effect traits – as for response traits, except excluding vagility and nest type and including flocking behaviour. We considered each of these traits to be relevant to the spatial scale of our analysis, which focussed on responses and effects within individual orchards and their immediate surrounds (i.e. ‘local’ scale).

Decision Stage 3 (Fig. 1) requires empirically testing the hypothesised candidate response and effect traits against the environmental change and ecosystem service of interest, and we used RLQ analysis to complete this step. The response-trait RLQ indicated a significant relationship between environmental change and species traits ( $P = 0.03$ , permutation test). RLQ axis one and two accounted for 51% and 24% of the total co-inertia between the R and Q tables, respectively

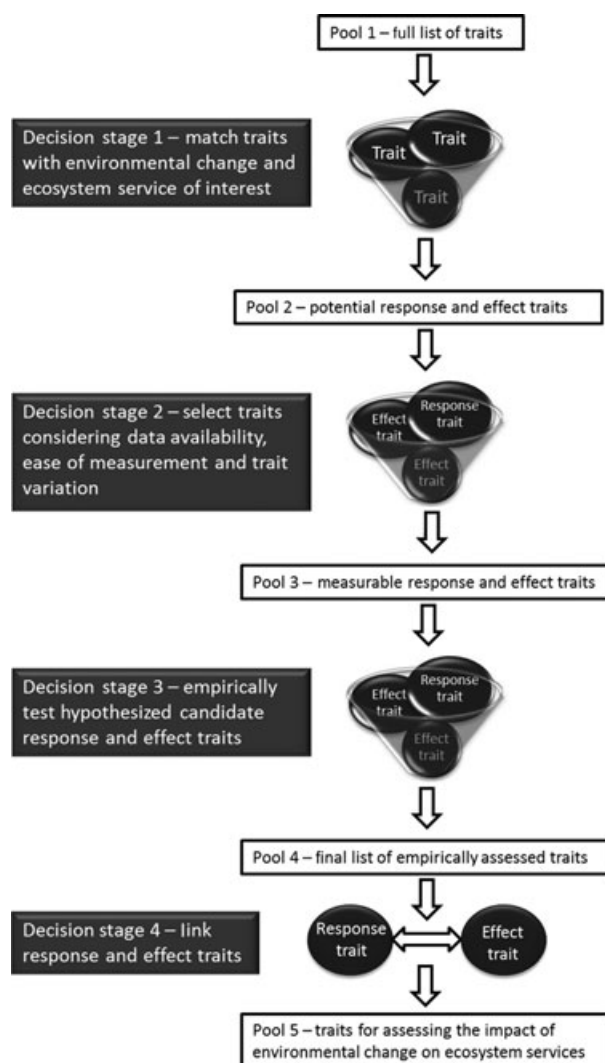


Fig. 1. Trait-selection framework.

**Table 1.** A list of avian traits that may dictate a species' response to environmental change or effect on ecosystem functions or services

Trait <sup>a</sup>	Response	Effect	Examples/notes <sup>b</sup>
<b>Morphological</b>			
Bill morphology (e.g. length, shape, depth)		✓	Influences pollination effectiveness, handling of fruit and seeds, and the type and location of food consumed
Gape width		✓	Dictates the size of seeds that can be consumed and dispersed, and the size of other food items (e.g. invertebrates)
Wing morphology (e.g. span, shape, loading, span/body mass ratio)	✓	✓	Aligned with movement capacity (e.g. local movements, dispersal and migratory status) which in turn influences resource use, seed dispersal and nutrient cycling, and the ability to respond to environmental change that disrupts landscape connectivity or reduces resource density
Tarsus/leg length		✓	Can influence foraging behaviour (e.g. where wading birds forage in intertidal areas) and hence services such as pest regulation and nutrient cycling
Feet morphology (e.g. size and shape)		✓	Can influence foraging behaviour (e.g. diving capacity of water birds) and small-scale nutrient cycling (e.g. scraping the ground to turnover soil)
Body mass	✓	✓	Strongly relates to a range of other traits in birds including metabolic rate, foraging behaviour, longevity and home-range size
Body shape		✓	Can relate to, for example, pest regulation by intimidation (e.g. silhouettes of birds of prey can alter the foraging behaviour of small vertebrates and reduce pest damage to crops)
Plumage colour/pattern		✓	Influences aesthetic appeal and can improve attractiveness to cultural services such as bird watching
<b>Physiological</b>			
Digestive physiology		✓	Gut retention time can influence the germination success of defecated seeds; acidic secretions in vulture stomachs facilitate feeding on decomposing waste
Metabolism (energy requirements)		✓	Interacts with plant nectar production to influence flower visitation by pollinators and gene flow among flowers
Relative brain size	✓		Related to behavioural flexibility and may reflect the capacity of species to adapt to novel environments or environmental change (Sol, Timmermans & Lefebvre 2002)
<b>Life-history</b>			
Diet (primary diet and dietary breadth)	✓	✓	Influences all aspects of foraging behaviour. Birds with specialised diets are susceptible to environmental change that reduces primary diet
Foraging behaviour (e.g. method, substrate, location, food handling and processing)	✓	✓	Impacts all aspects of resource use by birds. Species with particular foraging behaviours may be impacted by environmental change (e.g. stock grazing can negatively impact shrub-foraging birds; Martin & Possingham 2005)
Nesting behaviour (e.g. nest type, location, pair vs. colonial nesting)	✓	✓	Colonial-nesting seabirds transport nutrients from marine to terrestrial ecosystems and create substantial nutrient concentrations in particular locations. Hollow-nesting birds are negatively impacted by the logging of old growth forest (i.e. the loss of large, hollow-bearing trees)
Social behaviour (e.g. solitary, gregarious)	✓	✓	Birds that form flocks could have a greater localised impact on resource use (e.g. regulation of invertebrate pest outbreaks). Habitat loss and modification can disrupt the social dynamics (e.g. inter-territory interaction) of co-operative species (Luck 2002)
Mating behaviour (e.g. pair, cooperative breeding)	✓		Habitat loss and fragmentation can disrupt the cooperative breeding behaviour of some species (Luck 2002, 2003)
Reproductive behaviour (e.g. seasonality, time to first reproduction, chick rearing and feeding)	✓	✓	Reproduction may need to coincide with crop development and pest outbreaks to maximise the contribution of some species to pest regulation (e.g. Mols & Visser 2007). Climate change can alter the interactions between reproductive timing and food availability (Both & Visser 2005)
Reproductive effort (e.g. clutch size, breeding frequency, fecundity)	✓	✓	Species with low reproductive rates (e.g. small clutch size, infrequent breeding and low annual productivity) and low survival rates are less resilient to environmental change (i.e. have a reduced capacity to recover from perturbations). Species with large clutch sizes and/or large eggs may be preferred for food provisioning (e.g. consumption of eggs from domestic and wild fowl)
Survival rate (juvenile and adult)	✓		See above
Life span	✓		Long life span can be positively correlated with characteristics such as small clutch size and infrequent breeding, leading to a reduced capacity to recover from perturbations

Table 1. (continued)

Trait <sup>a</sup>	Response	Effect	Examples/notes <sup>b</sup>
Habitat use (primary habitat and breadth of habitats used)	✓	✓	Dictates where birds will conduct their activities. Habitat generalists appear more resilient to environmental change as they have greater habitat use options
Home range size	✓	✓	Can dictate the areal extent of an individual's activities (particularly for territorial species). Birds that need to maintain larger home ranges may be more susceptible to decline through the loss or fragmentation of their preferred habitat
Local movements		✓	Movements during day to day activities affect the contribution to services such as pollination, pest regulation and seed dispersal
Dispersal strategy (e.g. movement routes, distance, gender bias)	✓	✓	Where, when and for how far birds disperse can affect, for example, long distance seed dispersal. Birds with limited dispersal capacity (e.g. short distances or movements confined to certain vegetation types) may suffer more from reduced landscape connectivity
Migratory status (e.g. sedentary, partial migrant, seasonal migrant, nomadic)	✓	✓	Can influence large-scale cycling of nutrients and the delivery of services across broad regions
Perching behaviour		✓	Where birds perch and defecate seeds can affect seed germination and seedling survival
Competitive ability	✓	✓	In Australia, large/aggressive species (e.g. noisy miner <i>Manorina melanocephala</i> ) can exclude smaller species from vegetation patches leading to outbreaks of invertebrate pests and influencing pollination dynamics (Piper & Catterall 2003). Many of these species are also very adaptable to human-induced environmental change such as the expansion of agriculture or urbanisation

<sup>a</sup>Collective trait categories (e.g. bill morphology) are presented occasionally for the sake of brevity. The list of traits was derived from information contained in extensive reviews of the relationships between avian characteristics and environmental perturbations (e.g. Collar 1997) and ecosystem functions (e.g. Sekercioglu 2006a,b), other literature (example references are provided in the table where appropriate), expert opinion (see Acknowledgements) and our own ecological knowledge.

<sup>b</sup>The purpose of this column is to provide examples of why a particular trait may be considered a response or effect trait and to encourage others to consider their own examples and justification for the inclusion of traits in a particular analysis. Our examples are not meant to be exhaustive; particular traits may influence other aspects of species ecology, and we do not deal with interactions among traits (e.g. inter-trophic interactions that influence foraging behaviour) or broader issues of ecological complexity (see Discussion).

(see Appendix S1 for further summary results). We plotted the eigenvalues for tree cover and each trait variable along RLQ axes one and two to identify individual trait–environment relationships. For example, along RLQ axes one and two, tree cover was positively related to the abundance of species that had either a generalist diet or included pollen and nectar in their diet, and species that engaged in flexible (multiple) foraging behaviours, and along RLQ axis two, tree cover was positively related to species that used foliage as a foraging substrate (Fig. 2a).

The effect-trait RLQ indicated a significant relationship between the ecosystem service (represented by foraging rate) and species traits ( $P = 0.02$ ), and RLQ axis one and two accounted for 42% and 31% of the total co-inertia between the R and Q tables, respectively (Table S3). We plotted the eigenvalues for foraging rate and each trait variable. Foraging rate was, for example, positively related to species that engaged in hawking or sallying foraging behaviours, or used the air as a foraging location, along RLQ axes one and two (Fig. 2b). The result of these analyses is the identification of demonstrable links between the specific environmental change or ecosystem service of interest and particular species traits (i.e. Pool 4; Fig. 1).

The critical final step in the framework (Decision Stage 4) is to examine the links between response and effect traits (see Linking response and effect traits). This will result in a final set of traits that may be used predictively to assess the consequences of environmental change for the provision of ecosystem services (Pool 5; Fig. 1). In our case study, it is evident that, for example, increasing tree cover and foraging rate are both positively related to bird species that forage in the air and use hawking and sallying foraging behaviours (e.g. pursue invertebrates in continuous flight or from a perch). That is, as tree cover increases around apple orchards so does the abundance and foraging activity of these species. This may help to reduce the abundance of aerial invertebrate pests to apples such as the adult stages of codling moth, *Helicoverpa* moths, dimpling bug and fruit flies. However, different avian species are needed to control terrestrial or arboreal invertebrate pests (e.g. the larvae stages of moths). Therefore, based on our results, we predict that changes in tree cover around apple orchards may have only a limited impact on invertebrate pest regulation by birds. Improving the delivery of this ecosystem service may require the provision of suitable avian habitat (e.g. nesting sites) within orchards (e.g. see Mols & Visser 2007).



**Table 2.** Traits relevant to the environmental change (variation in tree cover) or ecosystem service (invertebrate pest regulation) studied (also see Appendix S1 in Supporting Information)

Traits	Variation in tree cover	Invertebrate pest regulation	Justification
Morphological			
Bill morphology		✓	Relates to diet and food handling
Gape width		✓	Relates to size of food items that can be consumed
Wing morphology	✓	✓	May indicate capacity to use open spaces (e.g. less tree cover) or manoeuvre through dense foliage (e.g. foraging in canopies of apple trees)
Body mass	✓	✓	Relates to metabolism, foraging behaviour and territory size
Physiological			
Relative brain size	✓		May indicate capacity to adapt to environmental perturbations
Life-history			
Diet	✓	✓	Type of food items consumed; those reliant on resources from trees (e.g. nectar) may be adversely affected by loss of tree cover
Foraging behaviour	✓	✓	Food procurement methods and foraging locations (e.g. tree canopy, shrub or ground layer)
Nesting behaviour	✓		Location of nests
Social behaviour		✓	Species forming flocks may have a greater impact on reducing invertebrate populations
Reproductive behaviour		✓	Reproductive timing may be critical to pest regulation (see Table 1)
Habitat use	✓	✓	Principal habitat requirements and capacity to use various habitats
Home range size	✓	✓	Relates to area over which a species forages
Local movements	✓	✓	Movements made by species in their day-to-day activities reflecting capacity to cope with tree loss or navigate through apple orchards
Dispersal strategy	✓		Relates to capacity to cope with loss of landscape connectivity
Competitive ability	✓	✓	Aggressive species may exclude other insectivores and may have greater capacity to adapt to environmental perturbations (see Table 1)

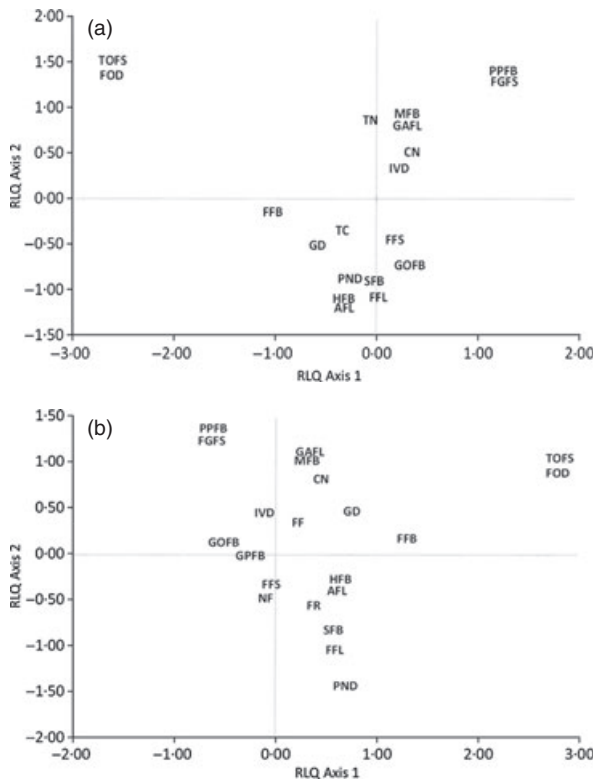
## Discussion

A substantial amount of progress has been made in the theoretical and empirical development of trait-based frameworks aimed at understanding the relationships between environmental change, plant communities and ecosystem function. Aspects of these frameworks are transferable to vertebrate communities, but key issues need to be addressed to ensure the frameworks are broadly applicable or are modified to suit particular vertebrate characteristics (e.g. greater mobility). We take an important, but first step in this direction by presenting a transparent and systematic decision process for selecting vertebrate traits that considers the interactions among environmental disturbances, species traits and ecosystem services.

We provided a simple empirical example with the principal aim of illustrating the trait-selection process, as opposed to examining comprehensively the implications of ecosystem change for service provision in our study area. Various landscape changes may influence bird response including changes in vegetation type or structure, the spatial distribution of habitat components (e.g. level of connectivity), food availability or intra- or inter-specific interactions including com-

petition or predation. Moreover, bird response may not be closely related to species traits. Accounting for the interactive effects of multiple environmental changes on organism response and consequently ecosystem functioning remains a major challenge in ecology (Tylianakis *et al.* 2008) and is an important research priority for trait-based frameworks more broadly (Lavorel *et al.* 2007). More research in this area and, most importantly, greater consistency in the application of trait-based approaches to vertebrates will yield further valuable insights into the potential of trait approaches to predict the consequences of landscape change for ecosystem function and the provision of ecosystem services.

Trait selection based on ecological knowledge or evidence from the literature may be criticised for being too subjective. A more objective approach has been proposed based on identifying the most optimal set of traits from a wider pool using a statistical framework (Bernhardt-Römermann *et al.* 2008). This is advantageous because it can be used to find the most parsimonious number of traits. Yet, striving for statistical elegance may exclude ecologically relevant traits that do not meet quantitative criteria. Moreover, subjective judgements still exist in comprising the pool of traits from which



**Fig. 2.** Plot of the eigenvalues along RLQ axes one and two for: (a) the response-trait analysis with tree cover as the environmental change; and (b) the effect-trait analysis with foraging rate as the ecosystem service indicator. Only eigenvalues  $> 0.40$  are shown for clarity. AFL, air foraging location; CN, cavity nester; CUN, cup nester; FF, flexible flocking behaviour; FFB, flexible foraging behaviour; FFL, flexible foraging location; FFS, flexible foraging substrate; FGFS, foliage-ground foraging substrate; FOD, fruit-other diet; FR, foraging rate; GAFL, ground-air foraging location; GD, generalist diet; GOFB, glean-other foraging behaviour; GPFB, glean-probe foraging behaviour; HFB, hawk foraging behaviour; IVD, invertebrates-vertebrates diet; MFB, miscellaneous foraging behaviour; NF, nonflocking behaviour; PND, pollen-nectar diet; PPFB, pull/prise/tear foraging behaviour; SFB, sally foraging behaviour; TC, tree cover; TN, tree nester; TOFS, tree-other foraging substrate.

the most relevant ones are selected (i.e. the pool is unlikely to be an exhaustive list of all possible traits). Identifying the most parsimonious number of traits avoids over-fitting models and including traits of little importance to the response/effect. This is an important issue regardless of how traits are selected. However, these statistical methods are very recent and we urge that ecological knowledge still plays a key role in trait selection.

The fact that plant ecologists deal with a single, albeit broad, taxonomic group with similar structural characteristics (i.e. most plants have stems, leaves and roots), compared to vertebrates as a 'group', has likely contributed to the substantial progress made in developing widely applicable trait frameworks. Developing trait lists and frameworks for vertebrates that can be broadly applied faces two challenges. First is the substantial morphological and behavioural diversity among vertebrate groups. The question remains whether trait lists can be identified only for particular

groups (e.g. separate lists for mammals, birds and reptiles) or if there are certain traits that are applicable across groups. In the example used above, some traits are relevant only to birds (e.g. bill morphology); however, there are many that are applicable to all vertebrate groups (e.g. body mass, body shape, digestive physiology, foraging behaviour and habitat use) suggesting great potential in identifying a list of 'inter-group' traits. The second challenge faced by vertebrate ecologists is that, in many cases, species from different taxonomic groups contribute to a given service. For example, all vertebrate groups contribute to seed dispersal (Corlett 1998), although seed-dispersal capacity varies among species. Developing trait frameworks designed to assess the impact of environmental change on ecosystem service provision should consider the relative contribution of species from different taxonomic groups.

A major challenge for trait-based frameworks more generally is accounting for interactions among or within trophic levels and their impacts on multiple ecosystem services. Functional traits can influence intra- and intertrophic interactions consequently affecting ecosystem functions and services (Schmitz 2008). For example, the foraging behaviour of avian predators (e.g. falcons) may influence the foraging behaviour and foraging rate of insectivorous birds thus impacting on their contribution to invertebrate pest regulation. Moreover, the supply of an ecosystem service (or services) may be the result of multiple ecological processes associated with different trophic levels (de Bello *et al.* 2010). Individual species traits, functional diversity, food web structure and multi-trophic interactions can all intersect in complex ways to influence ecosystem functioning (e.g. Petchey *et al.* 2004).

While dealing with this complexity is daunting, it is not, in theory, intractable if trait linkages can be identified (Lavorel *et al.* 2009). Conceptual frameworks based on species traits that account for more complex ecosystem dynamics (i.e. multi-trophic interactions and multiple ecosystem services) are just emerging (e.g. Lavorel *et al.* 2009; de Bello *et al.* 2010). For these frameworks to be appropriately applied, the same theoretical and practical advances in trait analyses that have occurred in plant ecology over recent decades must also occur in animal ecology.

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## Supporting Information

Additional Supporting Information may be found in the online version of this article.

### Appendix S1. Supporting methods and results.

**Table S1.** List of traits for which data were collected on the bird species in our study area.

**Table S2.** Response and effect traits for which trait values were available from the literature.

**Table S3.** Summary of results from the RLQ analyses.

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