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REVIEW

Prescriptive and empirical principles of applied ecology

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Abstract: Applied ecology is the science of managing ecosystems for defined outcomes, such as conservation, sustainable harvest, and animal pest and weed control. Robust knowledge in science is often expressed as "principles". Principles in applied ecology have utility by assisting scientists and managers to evaluate current management and to plan future activities. Principles also have a unifying role by identifying general patterns and processes across a broad discipline. We review usage of the word principle in applied ecology by critically evaluating principles proposed previously. We identify and describe two principal uses of principles; first, a prescriptive principle defined here as a general guideline for applied ecological research and management, and second, an empirical principle defined here as a broad generalization based on replicated empirical observations and experiments. Principles proposed previously are invariably for particular applications and are not generic across applied ecology. The principles are consolidated here in a new set of 22 prescriptive and 3 empirical principles. The new principles are more comprehensive than those proposed previously and relate to all aspects of applied ecology, extending across conservation, sustainable utilization, and management of animal pests and weeds. The principles should assist applied ecologists and managers to achieve specific management objectives.

Key words: applied ecology, biodiversity conservation, biological control, diminishing returns, pest control, principle, sustainable utilization.

Résumé : L'écologie appliquée est la science de l'aménagement des écosystèmes pour définir les issues comme la conservation, la récolte durable et la maitrise des ravageurs et des mauvaises herbes. En science, on exprime souvent sous le terme de principe la connaissance robuste. Les principes en écologie appliquée sont utiles pour aider les scientifiques et les aménagistes à évaluer les aménagements actuels et à planifier les activités futures. Les principes jouent également un rôle d'unification en identifiant des patrons et des processus généraux couvrant une large discipline. Les auteurs passent en revue le mot principe en écologie appliquée, en évaluant de façon critique les principes précédemment proposés. Ils identifient et décrivent deux principaux usages des principes; d'abord un principe descriptif qu'ils définissent comme un guide général en recherche écologique appliquée et en aménagement et ensuite un principe empirique qu'ils définissent comme une large généralisation à partir d'observations et d'expériences empiriques répétées. Les principes jusqu'ici demeurent invariables et ne sont pas génériques pour l'ensemble de l'écologie. Les auteurs consolident les principes dans un nouvel ensemble de 22 principes prescriptifs et 3 principes empiriques. Les nouveaux principes sont plus inclusifs que ceux proposés auparavant et portent sur tous les aspects de l'écologie appliquée, allant de la conservation à la conservation durable et à la maitrise des ravageurs et des mauvaises herbes. Ces principes devraient aider les écologistes appliqués et les aménagistes à rencontrer des objectifs spécifiques d'aménagement. [Traduit par le Rédaction]

Mots-clés : écologie appliquée, conservation de la biodiversité, lutte biologique, diminution des retours, lutte contre les ravageurs, principe, utilisation durable.

Introduction

Applied ecology is the science of managing ecosystems for defined purposes, such as conservation, sustainable harvest, and management of insects, and other invertebrates, vertebrate pests and weeds, including through biological control. It aims to provide knowledge and understanding that can be drawn upon when planning, implementing, and assessing management actions within the broad discipline.

Robust knowledge in science is often expressed in "principles". So what are principles and do they matter? The Concise Oxford Dictionary definition of principle includes the following: a fundamental truth used as a basis of reasoning; or a general law as guide for action (Sykes 1976). In the Macquarie Dictionary principles are defined as follows: an accepted or professed rule of action or conduct; a fundamental, primary, or general truth, on which other truths depend; a guiding sense of the requirements and obligations of right conduct; a rule or law exemplified in natural phenomena (Anon 1990). The Dictionary of Environment and Ecology (Collin 2004) does not define principle per se but defines the competitive exclusion and precautionary principles using the key word idea. Two types of principles of ecology, one quantitative and the other a cause-and-effect relation, were suggested by Allee and Park (1939).

Do principles matter? Principles in applied ecology have utility by assisting scientists and managers to evaluate current management activities and plan future interventions. Environmental scientists and ecosystem managers often have to study or manage a particular species or ecosystem, in a particular habitat, using a particular method, at a particular time. Principles have a unifying role by identifying general patterns and processes across such a

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broad discipline of topics. Both inductive science and deductive science (Harre 1972; Romesburg 1981) are used to refine the generalizations through which applicable knowledge is expressed (Allee et al. 1949, p. 5). When such generalizations are available, they can be applied widely, including to populations and ecosystems different from those studied previously and from which the generalizations were derived. Thus principles can provide guidance to scientists and managers addressing novel problems or involving unfamiliar species or communities.

Principles have been proposed previously in ecology, for example, by Allee and Park (1939), Margalef (1963), Lawton (1999), Berryman (2003), Fierer et al. (2009), and Scheiner and Willig (2011). In applied ecology, principles have been proposed for particular applications: for example, for assessing impacts of construction of a dam (Walker and Norton 1982), evaluating sustainability of harvests (Ludwig et al. 1993), guiding land use (Dale et al. 2000), controlling pest damage (Hone 2007), conserving biodiversity (Steffen et al. 2009), selection and management of marine reserves (Ballantine 2014), and ensuring healthy freshwater ecosystems (Lapointe et al. 2014). Principles have been proposed in the related field of ecological design (Shu-Yang et al. 2004). The principles developed for these specific applications are not immediately applicable across the full breadth of applied ecology. We endeavour here to achieve that generality.

The aim of this paper is to review, and provide a synthesis of, the principles underlying applied ecology. Our approach is first to clarify the meanings and usages of the term principle and then to examine principles proposed previously that relate to applied ecology topics. Our synthesis is in the form of a new set of principles that is intended to be widely applicable. We emphasize here that this paper is concerned with applied ecology, not ecology per se, and so the principles primarily address management actions for defined purposes and the assessment of their effectiveness. They should not be confused with similar generalizations in ecology that focus on patterns and processes in species and ecosystems, without reference to management actions. It is our expectation that this work will engender some debate, and we welcome review and evaluation of our proposals.

Approach

We searched ecological journals, related books, and nonscientifically refereed ("grey") literature for use of the word principle. Searching was based on cited use of literature across all of the three main topics of biodiversity conservation, sustained utilization or harvest, and pest and weed control. The search was not exhaustive but sampled a relevant and representative range of literature, particularly over the years 1982–2014 inclusive. In some cases we found that while the word principle was used, sometimes in the title, no specific principles were stated or proposed explicitly; such works were not considered further in our review.

Definition and usage

The review of dictionary definitions of the word principle shows there is no single, clear definition. We take a principle to be a statement, expressed in general terms, of an important guideline or widely applicable truth, concerned with management activities. It should be applicable to many problems, species, ecosystems, and times. It should not be so vague that it falls into the "yawning abyss of vacuous generalities" (Cox 2007).

Our consideration of the literature has led us to propose, at least in applied ecology, that a distinction can usefully be made between two classes of principle. First, there are general guidelines or rules on how to develop and implement a management activity; and second, there are generalizations, developed from replicated observations and experiments, about how effective management activities are at achieving their aims. We call these prescriptive and empirical principles, respectively.

A prescriptive principle is an instance of the Oxford dictionary's "guide for action". The principle of parsimony (Burnham and Anderson 2001) and the precautionary principle (Burgman and Lindenmayer 1998; Olsen 1998; Chapman and Reis 1999) provide guiding frameworks in statistics and resource management, respectively (though the value of the precautionary principle is disputed, e.g., Cussen (2009)). Five ecological principles were used to propose eight guidelines for land-use decision making (Dale et al. 2000). The United Kingdom Biodiversity Action Plan was based on six principles (Anon 1994) that are prescriptive. The National Strategy for the Conservation of Biological Diversity in Australia (DEST 1996) described nine principles to be used as "guides for implementation of plans and actions" (Steffen et al. 2009); see also Lindenmayer et al. (2006). A set of 10 prescriptive principles was proposed for an updated Australian Biodiversity Conservation Strategy (Anon 2010). A more specific example is related to urban planning and threatened species (Williams et al. 1995), with the principles being used to "enable planners to assess alternatives" (Georges et al. 2008). Clear principles that "must guide policy" on a carbon price for climate change management were outlined by Garnaut (2011, p. 69). For threatened species and predator management, principles are used "to guide decision making" (Southgate 2014). Examples of principles proposed previously within the general context of applied ecology, and that we deem to be primarily prescriptive, are listed in Table 1.

Some prescriptive principles are more than guidelines, as they express obligations or rules: for example, protocols that must be followed if a scientific investigation is to be deemed of high quality, or to achieve social acceptance or meet legal requirements. These are instances of the Macquarie dictionary's (Anon 1990) "rule for action or conduct". The principles of experimental design, randomization, replication, and control were described as "basic rules" for scientific investigation (Caughley and Sinclair 1994, p. 239; Sinclair et al. 2006, p. 287). The ethics principles of replacement, reduction, and refinement (Russell and Birch 1959; Anon 2004) are examples of obligations that ecological researchers and managers now have to meet.

An empirical principle is a generalization of replicated observations or experimental results that has been demonstrated to have widespread validity and application. For example, exploitation of a population reduces abundance, and the greater the exploitation the smaller the population becomes (Krebs 2001). The generalization is often derived by induction and evaluated by deduction, in the sense of Harre (1972) and Romesburg (1981), and thus incorporates both empirical and theoretical support. Such generalizations are probabilistic, stating an average result or pattern. Empirical principles should be based on reproducible evidence, and thus be testable, and hence either falsifiable (Popper 1963) or capable of being shown to have more or less support than alternative generalizations (Burnham and Anderson 2001). They are therefore hypotheses in the Popperian sense, though of a particularly general and wide scope. The cause-and-effect relations of Allee and Park (1939) are empirical generalizations. The "fundamental truth" of the Oxford (Sykes 1976) and Macquarie (Anon 1990) dictionaries is such a usage. Principles of this type have been described as a fundamental truth, as a proposition that can form the basis of reasoning (Allee and Park 1939), as a generalization (Allee and Park 1939; Allee et al. 1949; Watt 1973; Bailey 1984) or confirmed generalizations (Scheiner and Willig 2011), as general rules of conformation obeyed by all communities (Putman and Wratten 1984, p. 56), as the laws and rules of ecology (Lawton 1999), as repeated patterns (Ricklefs and Miller 2000; Begon et al. 2006), as fundamental components of theory and self-evident truths (Berryman 2003), and as a universal truth or a translation of physical–chemical laws (to ecological systems) (Krebs 2009).

In summary, many principles relating to applied ecology have been proposed, but they have been developed usually for particular contexts, such as only for biodiversity conservation, and have

Table 1. Examples of prescriptive principles in applied ecology, in their original wording, grouped according to their field of application.

General
• Precautionary principle. Where there are threats of serious irreversible environmental damage, lack of full scientific certainty should not be used as a reason for postponing measures to prevent environmental degradation[1]
Biodiversity management
• Species should continue to live in their current locations[2]
• Offsets can help species to survive somewhere else[2]
• Maintain viable population sizes and facilitate increases where feasible[2]
• Maintain well-functioning ecosystems[2]
• Remove or minimise existing stressors[2]
• Manage appropriate connectivity for species, landscapes, seascapes and ecosystem processes[2]
• Protect a representative array of ecological systems[2]
• Where biological resources are used, such use should be sustainable[9]
• Wise use should be ensured for nonrenewable resources[9]
• The conservation of biodiversity requires the care and involvement of individuals and communities as well as Governmental processes[9]
• Conservation of biodiversity should be an integral part of Government programmes, policy and action[9]
• Conservation practice and policy should be based upon a sound knowledge base[9]
• The precautionary principle should guide decisions[9]
• Representation. A system of marine reserves to maintain the full range of marine life must include representative reserves in all regions and each major habitat in each region[10]
• Replication. Within each region and major habitat there should be several spatially separated marine reserves[10]
• Geographically widespread network. With a network of marine reserves, eggs and larvae from one reserve can drift to and supply other reserves[10]
• Self-sustaining total area. The system must be sufficiently large in area to maintain itself through time, independently (as far as possible) of the surrounding seas[10]
Biodiversity conservation by landscape restoration
• Analyze the causes of landscape dysfunction[3]
• Restore ineffective processes sequentially[3]
• Monitor indicators reflecting landscape processes[3]
Sustainable utilization
• Sustainability. Meet the needs of the present without compromising the ability of future generations to meet their own needs[4]
• Include humans as part of the system[5]
• Act before scientific consensus is achieved[5]
• Rely on scientists to recognize problems, but not to remedy them[5]
• Distrust claims of sustainable resource use[5]
• Confront uncertainty[5]
• Examine impacts of local decisions in a regional context[6]
• Plan for long-term change and unexpected events[6]
• Preserve rare landscape elements and associated species[6]
• Avoid land uses that deplete natural resources[6]
• Retain large contiguous or connected areas that contain critical habitats[6]
• Minimise the introduction and spread of non-native species[6]
• Avoid or compensate for the effect of development on ecological processes[6]
• Implement land-use and management practices that are compatible with the natural potential of the area[6]
• Sustainability has many conflicting definitions and the choice depends upon the objectives[7]
• It is better to monitor the population than the harvest[7]
• Exploit conservatively[7]
• Population growth rate is usually mismeasured[7]
• Density dependence is essential[7]
• Quantifying density dependence is exceedingly difficult[7]
• Population increase can be exploited[7]
• Sustainable exploitation involves reducing population size[7]
• Quotas are unstable[7]
• Increasing effort is simple, reducing it is painful[7]
Pest management
• Consistency with the principles of Ecologically Sustainable Development[8]
• Adoption of beneficiary pays[8]
• Managing the inherent variability of land management systems[8]
• Defining the role of various policy instruments to ensure desired management goals are met[8]
• Involving all major interest groups in ownership of pest problems, and in planning and implementing management programs[8]
• Managing total grazing pressure[8]
• Considering animal welfare[8]

Note: The list reflects the broad scope of fields and principles though it is not exhaustively comprehensive. Sources:
[1]Burgman and Lindenmayer (1998).
[2]Steffen et al. (2009).
[3]Tongway and Ludwig (2011).
[4]WCED (1987).
[5]Ludwig et al. (1993).
[6]Dale et al. (2000).
[7]Sutherland (2001).
[8]Braysher (1993), Olsen (1998).
[9]Anon (1994).
[10]Ballantine (2014).

limited wider applicability. Moreover, they are expressed in widely varying styles, range in form from detailed to vague, and no individual set published to date could be regarded as complete. Nevertheless, these previous contributions, as an ensemble, have provided the basis for the new and comprehensive set of general principles that we present in the following section.

Prescriptive principles — review and synthesis

Most of the prescriptive principles we have identified from earlier publications have been developed for a particular application, for example, dam construction, land use allocation, or stream flow manipulation (Table 1). As is to be expected, some are specific while others appear (in slightly different forms) in more than one of the sources. Many of the duplicated principles are concerned with general issues and have wide applicability. We first combined the similar principles and restated them, and also some of the specific principles, in a more consistent style, and organized them in categories. We brought all of the more general principles into a single category. On examining the revised list, we concluded that the scope of the majority of the revised principles was still too narrow. We therefore sought to identify the key themes contained in these statements and to re-express them in general terms. The resulting new prescriptive principles are organized into only two thematic categories: one covering social and governance issues and the other ecosystem management. Principles in the second category have their basis in the underlying science of ecology, and they aim to encapsulate generalizations developed within that discipline that are relevant to ecosystem management. In formulating this list, we have endeavoured to express the new principles simply, yet avoid them being so general as to be devoid of meaning. A criterion for inclusion has been that the principle is practical. The final number of principles results from the aim that the list be comprehensive and our decision to avoid artificial combinations.

New prescriptive principles of applied ecology

In the text below the new principle is the first sentence after the principle's name. Most principles are self-explanatory, but sometimes a brief explanation or example has been appended. Sources of the published principles are given in Table 1.

Principles relating to social and governance issues

1. **Law principle**: Management actions must comply with all applicable legislation and regulatory requirements.
2. **Ethics principle**: Management actions must be conducted openly and deal fairly with all stakeholders, and aim to minimize suffering by sentient animals.
3. **Sharing principle**: Lands and populations have stakeholders with differing interests and cultural perspectives that must be acknowledged and supported in management.
4. **Politics principle**: Decisions involving trade-offs between ecosystem management and social values fall outside the realm of ecological science and are properly the business of government.
5. **Evidence principle**: Management decisions should be based on current scientific evidence and recognize that the available scientific evidence develops over time.
6. **Knowledge principle**: Investigations and monitoring to increase knowledge will generally be needed to develop and evaluate management actions. Such monitoring is necessary as knowledge of ecosystems is often poor and ecosystems are dynamic.
7. **Uncertainty principle**: Management should recognize, accept, and accommodate a degree of uncertainty in the information available for planning and decision making. Ecosystems are complex and full knowledge of their response to management is unachievable.
8. **Precautionary principle**: When trend data, ecological theory, or observations of similar systems indicate that the consequences of inaction might be severe, immediate intervention based on general theory is appropriate; and when a proposed action is likely to be irreversible, evidence that it will not have undesired consequences must be particularly strong.

Principles relating to ecology and ecosystem management

9. **Theory principle**: Management strategies and actions should be consistent with general ecological theory. Ecosystem structure and functioning are broadly understood and this knowledge should underlie the design and formulation of management actions.
10. **Priority principle**: Prioritize management aims and implement adaptive management options that produce the greatest desired effects, relative to the ease or difficulty of management implementation.
11. **Review principle**: Review management interventions regularly, drawing on ecosystem monitoring and changes in knowledge, and adapt as appropriate using criteria for assessing management success or failure.
12. **Change principle**: Recognize that ecosystems are dynamic, and expect that management strategies and actions need to be adaptive. Change may arise in ecosystems in response to management actions through learning or adaptation by the target organism, or in response to external factors, such as modification of adjacent areas and climate change.
13. **Physical landscape principle**: Management strategies and actions should recognize rock type, landforms, soils, groundwater, and surface water flows, and may include remediation or modification of these.
14. **Ecosystem principle**: Manage to maintain ecosystem features and processes and to conserve indigenous biodiversity (the variety of life). Organisms are adapted for life within specific ecosystems and depend on such ecosystem features and processes and directly or indirectly on many other organisms.
15. **Genetic diversity principle**: Recognize the genetic diversity within a population and manage to maintain it and the evolutionary potential for adaptation that it confers.
16. **Mobility principle**: Recognize that many species migrate or move between multiple habitats and extend management to apply through their entire life cycle and range. Assisted movement may be an appropriate response to habitat fragmentation or climate change.
17. **Scale and connectivity principle**: Manage at the landscape scale, employing connectivity to avoid population and community fragmentation and natural or artificial barriers to isolate vulnerable populations and prevent the spread of undesirable species. Protection of small, isolated, areas may not be sufficient to ensure population and community survival, but such areas can also provide refuges within which elimination of pest species may be practical.
18. **Robustness principle**: Manage for extreme events, such as droughts and hurricanes; allow for the variance around the average and never assume that current or average conditions will continue. Populations and ecosystems exhibit varying degrees of stability and have limited resilience.
19. **Unintended consequences principle**: Be alert for unforeseen ecosystem responses to management interventions and modify actions that produce undesirable side-effects. As well as direct effects, such as nontarget kills during pest control, undesirable changes may arise through the internal interactions and dependencies in ecosystems or through evolution by natural selection (see empirical principles 2 and 3 below).
20. **Sustainability principle**: Management actions should aim to shift an ecosystem to a state where it is self-sustaining and further interventions are minimized.
21. **Human use principle**: Integrate utilization into ecosystem management, encouraging uses that are synergistic with conservation and biodiversity objectives and holding inimical activities to a level low enough for system integrity to be maintained. The same general principles of ecosystem and landscape management apply in natural, modified, and agricultural or urban environments.
22. **Taxonomy principle**: Identification and naming of taxa subject to management is a priority. A scientific name is often a prerequisite for legislation and effective regulation including declaration of a taxon as threatened or endangered. Recognizing cryptic taxa is essential for effective management. This principle was not found in previous publications.

Empirical principles — review and synthesis

As for the prescriptive principles we collated examples of published principles (Table 2) and edited and combined them where appropriate. As the resulting list was again long and the principles still mostly focused on particular applications, we developed a more general set.

Our new set of empirical principles has only three candidate members. There may be additional empirical principles that remain to be identified: for example, general statements or hypotheses about management of connectedness, or of genetic diversity, or dealing with one of the other themes identified in the set of prescriptive principles, can probably be proposed. However, we will confine our considerations to the three generalizations that follow. As above, the principle is the first sentence. For these testable hypotheses, however, the discussion is more extensive than was required for the prescriptive principles above.

1. **Effort–outcomes principle**: There is a cause-and-effect relationship between the desired outcomes of management and the effort applied (the inputs), but with diminishing returns.

Table 2. Examples of empirical principles in applied ecology, in their original wording, grouped according to their field of application.

Biodiversity management

- The ecological relationships that link impacting activities to ecosystem features of concern are usually nonlinear[1]
- Degradable compounds introduced into an ecosystem can be decomposed or assimilated, up to a certain rate of introduction[1]
- Persistent compounds (such as DDT and heavy metals) accumulate with trophic distance, highest concentrations being found in top carnivores[1]
- Flow is a major determinant of physical habitat in streams, which in turn is a major determinant of biotic composition[2]
- Aquatic species have evolved life history strategies primarily in direct response to the natural flow regimes[2]
- Maintenance of natural patterns of longitudinal and lateral connectivity is essential to the viability of populations of many riverine species[2]
- The invasion and success of exotic and introduced species in rivers is facilitated by the alteration of flow regimes[2]

Sustainable utilization

- Stable ecosystems are not likely to absorb the perturbations induced by harvesting without catastrophic effects[1]
- Exploitation of a population reduces its abundance, and the greater the exploitation the smaller the population becomes[3]
- Below a certain level of exploitation, populations are resilient and compensate for removals by surviving or growing at increased rates[3]
- Exploitation rates may be raised to a point at which they cause extinction of the resource[3]
- Somewhere between no exploitation and excessive exploitation is a level of maximum sustained yield[3]
- Laws of physics and chemistry apply to ecology[5]
- Population dynamics are regulated by reproduction, mortality, and growth[5]
- Habitat quantity and quality are prerequisites for fish productivity[5]
- Connectivity among habitats is essential for movements of fishes and their resources[5]
- Freshwater species and their habitats are tightly linked to surrounding watersheds[5]
- Biodiversity can enhance ecosystem resilience and productivity[5]
- Global processes affect local populations[5]
- Anthropogenic stressors have cumulative effects[5]
- Evolutionary processes can be important[5]

Pest management

- When a population is subject to severe stress (for example when exposed to pesticides or disease), the effect on individuals within that population will be variable. Since this variability, at least in part, is due to genotypic differences, impacts that are persistent, or which recur frequently, will cause a selection for genotypes that are adapted to and survive this stress[1]
- Compared with “r-pests”, pests falling in the K-category are usually far more susceptible to manipulation of their numbers, and are often more sensitive to interference with their environment[1]
- Removal of species from an ecosystem consequently leads to an expansion in the abundance and distribution of their competitors[1]
- Response, for example yield, is negatively related to pest damage[4]
- Pest damage is positively related to pest abundance [4]
- Pest abundance is reduced, with diminishing returns, by control efforts[4]
- As pest control reduces pest abundance, cost per removal increases exponentially[4]
- Response, for example yield, is positively related, with diminishing returns, to control efforts[4]
- Over time, pests evolve responses to control efforts[4]

Note: The list reflects the broad scope of fields and principles though it is not exhaustively comprehensive. Sources:
[1]Walker and Norton (1982).
[2]Bunn and Arthington (2002).
[3]Krebs (2001).
[4]Hone (2004, 2007).
[5]Lapointe et al. (2014).

The effort–outcomes relationship is of utility to conservation, sustainable utilization, and animal and weed pest management, including biological control. The relationship is often implicit but needs to be explicit. It is a generalization of relationships that have been proposed previously: in pest control, the total revenue to inputs relationship (Conway 1981, fig. 15.1), in biodiversity conservation, the species maintained to investment relationship (Wilson et al. 2007; Grantham et al. 2008), the probability of change in the International Union for Conservation of Nature (IUCN) Red List category of a species to management expenditure (McCarthy et al. 2008), and the extinction probability to management inputs relationship (McDonald-Madden et al. 2008). Our statement of the relationship includes the feature of diminishing returns, the progressive reduction in outcomes (benefits) for each higher level of inputs (effort), a principle established in both agricultural (Blake 1968) and general (Gans et al. 2009) economics. The effort–outcomes principle is a general, testable, empirical relationship that focuses on the effects of management actions and other human impacts (e.g., traditional harvesting), and we consider it fundamental to applied ecology. This new empirical principle has apparently not been described previously in so general a form. For example, the principles of Walker and Norton (1982) are not explicit about the input–outcome relationship. The closest is their principle 9 (Table 2) describing nonlinear effects of impacting activities on an ecosystem that in our version appears specifically as diminishing returns. The principle is consistent with the need for testing practical methods described by Sutherland et al. (2013).

Empirical evidence: Empirical examples of the relationship are few. One example is the linear, positive, relationship between the temporal change in abundance of black rhinoceros (*Diceros bicornis*) and the costs of anti-poacher patrols in a part of Zambia and also across nine African countries (Leader-Williams and Albon 1988). Similar positive relationships were reported therein for African elephant (*Loxodonta africana*). Positive relationships between changes in abundance and measures of governance and corruption across a range of African countries have been reported for those two species (Smith et al. 2003). Positive linear relationships occurred between the temporal trends in bird abundance in European countries relative to those in the United Kingdom and the percentage of land designated as special protection areas (Donald et al. 2007). These positive linear relationships must be part of a curve (concave down), as the annual population growth rate of any species must have a maximum value determined by maximum fecundity and survival rates (Berryman et al. 1995; Hone et al. 2010).

Several studies provide evidence of a negative, curved relationship between outcomes and management effort. The density of moose (*Alces alces*) was negatively related to hunting effort (hunter days km^{-2}) in Quebec, Canada (Crete et al. 1981, table 2). In southeastern Australia, lamb kills by red foxes (*Vulpes vulpes*) were negatively related to the level of fox control (Greentree et al. 2000, table 3). Poaching pressure (effort) for large mammals was negatively related to budgets in the Serengeti National Park (Hilborn et al. 2006, fig. S2). The national prevalence of bovine tuberculosis (bTB: *Mycobacterium bovis*) in livestock was negatively related to the annual costs of brushtail possum (*Trichosurus vulpecula*) control in New Zealand (Hone 2013, fig. 4). Changes in abundance of red (*Cervus elaphus*) and sika (*Cervus nippon*) deer (both pests) in parts of New Zealand were negatively related to hunting effort using helicopters (Forsyth et al. 2013, fig. 7). We propose that such negative relationships have dependent (*y*) variables that are not management outcomes themselves but are variables that are intermediate steps towards the desired outcomes. For example, lower pest density, following pest control or harvesting, should lead to higher agricultural production or higher density of endangered species, and these latter variables are the desired outcomes. Harvesting increases the hunters' utility (their satisfaction with the activity) and can lower population density of the hunted species, but the lower density is not the desired outcome of hunting.

2. **Ecosystem responses principle**: Ecosystems undergo trophic change in response to management actions.

   The principle is a generalization of the pest replacement principle (Table 2) of Walker and Norton (1982) to relate also to conservation and sustainable utilization. The principle is linked to the effort–outcomes principle because while the management aim may be to decrease abundance of one species, the outcomes may include an increase in abundance of another species as a result of trophic restructuring and trophic cascades. The principle forms part of the empirical evidence for the new prescriptive unintended consequences principle, though that is also supported by general ecological science.

   Empirical evidence: There are many examples of this principle. Predator (red fox) control to reduce effects of predation on native wildlife resulted in increased abundance of European rabbits (*Oryctolagus cuniculus*) in a part of southeastern Australia (Banks et al. 1998). The biological control of insect pests of cotton by growing of transgenic *Bt* cotton in parts of China was correlated with an increased abundance of a nontarget insect species (mirid bug; Heteroptera: Miridae) that itself became a pest (Lu et al. 2010). Control of brushtail possums in a part of New Zealand to reduce bovine tuberculosis (bTB) in domestic livestock resulted in increases in abundance of rats (*Rattus rattus*) two years after treatment (Ruscoe et al. 2011). Control of dingoes (*Canis dingo*) in forested parts of Australia to control livestock predation resulted in increased fox abundance amongst other effects (Colman et al. 2014).

3. **Evolution principle**: An evolutionary response will arise to management actions if these are sustained, and usually this will reduce their effectiveness.

   The empirical principle (Table 2) that pests evolve responses to management actions (Walker and Norton 1982; Hone 2007) can be generalized to relate to biodiversity and sustainable utilization objectives. The concern here is with genetic responses rather than the ecosystem responses described in the previous principle.

   Empirical evidence: There are many examples related to this principle. A fish species, Atlantic silverside (*Menidia menidia*), with the largest individuals being culled selectively, evolved towards smaller size (Conover and Munch 2002). Harvesting of bighorn sheep (*Ovis canadensis*) with larger horns led to evolution of sheep with smaller horns (Coltman et al. 2003). Resistance to herbicides (Helander et al. 2012; Delye et al. 2013) and to pesticides (Buckle 2012) has occurred in many species. A more involved example is the co-evolution of myxoma virus and European rabbits after virus introduction to Australia and Britain to control the rabbits and their agricultural and environmental impacts (Fenner and Ratcliffe 1965; Fenner 1983).

Conclusions

The operational work of applied ecologists comprises the management of species and ecosystems with at least one of the aims of conserving biodiversity, harvesting sustainably, and minimizing pest and weed damage. Management strategies and actions can be guided by a set of general principles that encompass social and ecological requirements. Hence, principles have both a utility and a unification role in applied ecology. We have reviewed many such principles proposed previously and found they can be generalized and formulated in uniform style and that a comprehensive new set can be developed. These new principles fall into three groups: the first two are prescriptive in nature (the first being concerned with social and governance issues and the second with ecosystem management), and the third empirical. The empirical principles are generalizations of the results of research on the effectiveness of ecosystem management and on its unintended effects, and they can be regarded as hypotheses for testing. There are few studies of the relationship in the effort–outcomes principle, while reports of unintended consequences, involving both trophic and evolutionary responses, are numerous. We encourage and challenge applied ecologists to evaluate the principles presented here, and to identify additional candidates.

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