

REVIEW

One hundred years of population ecology: Successes, failures and the road ahead

Charles J. KREBS

Department of Zoology, University of British Columbia, Vancouver, Canada and Institute for Applied Ecology, University of Canberra, Canberra, Australia

Abstract

Population ecology is the most mature of the three subdisciplines of ecology partly because it has a solid mathematical foundation and partly because it can address the primary questions of distribution and abundance with experimental protocols. Yet there is much left to do to integrate our population knowledge into community and ecosystem ecology to help address the global issues of food security and the conservation of biodiversity. Many different approaches are now being developed to bring about this integration and much more research will be necessary to decide which if any will be most useful in achieving our goals of explaining the changes we see in the distribution and abundance of animals and plants. Food web ecology would appear to be the best approach at present because it uses the detailed information of the population ecology of particular species in combination with data on consumer–resource interactions to apply to the applied problems of biodiversity conservation, food security, pest management and disease prevention. If we can use our understanding of population ecology to address the practical problems of our time in a creative way, we will benefit both the human population and the Earth's biodiversity. Much remains to be done.

Key words: abundance, geographic distributions, history of ecology, population models

Correspondence: Charles J. Krebs, Department of Zoology, University of British Columbia, 6270 University Blvd., Vancouver, B.C. V6T 1Z4 Canada.
Email: krebs@zoology.ubc.ca

INTRODUCTION

Population ecology has come a long way since the days of Charles Elton and all the early ecologists (Crowcroft 1991). Writing the history of how any science has changed in a century is a difficult process because any one individual sees only one slice of what has transpired. (McIntosh 1985; Kingsland 2005). In this review I will try to discuss the general problems that population ecology addresses and how well it has accomplished solving these problems over the past century. On the way I will point out what I think are the failures of the past if only to try to avoid repeating them in the future.

The number of ecologists in the world continues to increase in an approximate exponential manner. Along with this increase is a scientific fragmentation that must occur because one person cannot know everything, so we become aquatic ecologists or biological control specialists or ecological geneticists or conservation biologists, and we concentrate on one small part of the ecological spectrum. This leaves open the problem of missing vital information that is buried in the literature that now seems ancient, or in journals no longer published or not available electronically, or in people working on the other side of the world and not publishing in English. All of these issues make assessing the successes and failures of ecology problematical. This apology now given, I will charge ahead to try to describe what I think ecologists wish to achieve and how far they have achieved it. I concentrate on population ecology, which I know most about, but also because it is the best developed of the ecological subdisciplines and significantly ahead in understanding when compared with community and ecosystem ecology. I will not say much about microbial ecology, a rapidly moving field about which I know little.

THE GOALS OF POPULATION ECOLOGY

The goal of population ecology is to understand the reasons for the distribution and abundance of microbes, plants and animals. This was the message of Charles Elton (Elton 1927) and Andrewartha and Birch (Andrewartha & Birch 1954). The best achievement would be to be able to predict changes in distribution and abundance as critical environmental factors change. However, prediction is not always possible, even if we have a solid understanding of the mechanisms causing ecological changes in distribution and abundance. Similar problems are well recognized in geology with regard to earthquake predictions (Uyeda 2013). The end goal of ecological research is both to protect the Earth's biodiversity and to increase the quality of life for all people through ecosystem management. Both these goals can be achieved only by managing people as well as understanding natural processes, goals that have long been recognized in fisheries management (Hilborn 2007).

There is a nearly universal critique of ecology which suggests that our science is achieving these goals very slowly (Peters 1991; O'Connor 2000; Graham & Dayton 2002). It is difficult to evaluate this general cri-

tique because the metric of "progress" is not quantified. Progress in any science depends in part on the number of scientists working in an area, the time scale of the events and processes that require explanation, and the money available to carry out the necessary experiments. It is relatively easy to point out that all 3 of these components of the rate of progress are at the low end of the scale for ecology. Funding for ecological research is growing but the problems facing us are perhaps growing at an even faster rate. The bottom line is that if we are convinced that ecology is achieving its goals too slowly, we require some suggestions for how to improve the science. Peters (1991) offered some suggestions but received mainly brickbats in return (Lawton 1991). Ecological critics can be easily offended but the main point of criticism is to generate discussion.

GENERALITY IN POPULATION ECOLOGY

Ecologists, like all scientists, wish to generalize their results, and this is highly desirable. The problem we face is that we do not know the domain of applicability of any particular finding. While we have global theories that predominated in the 1960s and 1970s, we are now in a stage of global confusion which has arisen because of detailed local studies that reach opposite conclusions about particular ecological processes. The classical example is the controversy over density-dependent regulation of population size. The models are mostly simple but the empirical results are not and we do not know what to do with populations that show density-vague relationships (Strong 1986). Beautiful hypotheses and ugly facts, Dennis Chitty labeled it (Chitty 1996).

What do we do with data that do not fit any particular hypothesis? There are two possible approaches. First, ignore the contrary data. In the words of one famous ecologist to me years ago, "We do not refute our critics, we simply ignore them." There may be several important reasons for ignoring results (e.g. faulty equipment, faulty experimental designs and faulty logic) and these must be investigated. However, the second approach is more useful in the long run: change the domain of applicability of the hypothesis or reformulate it. There is a good example of this approach in the evaluation of the intermediate disturbance hypothesis for plant populations (Kershaw & Mallik 2013) and whether this hypothesis applies only in certain specific kinds of plant communities.

One key reason for contrary results is that the scale

of the study or the experiment is not properly designed to test the question at hand. Very often we make these design errors first and then only later discover the problems of interpreting the resulting data. This kind of problem is clearly seen in studying the social organization of rodents in which data from small pens do not mimic those obtained from large pens or open field studies (Wolff & Sherman 2007). Landscape ecology is difficult and we rarely have the resources to conduct these large-scale experiments (Lidicker 1995). Nevertheless, they must be done to reach generality in population studies and methods are now being developed to achieve this goal (Borer *et al.* 2014).

SUCCESSSES IN POPULATION ECOLOGY

There are four broad categories of success that population ecology has achieved during the past century and I will review each of them in turn.

Mathematics of populations

Science progresses when it bonds with mathematics, and population ecology is the strongest of the sub-disciplines of ecology in its mathematical development (Ginzburg *et al.* 2007). The key to all of this is that there is a mathematics of populations, developed largely by human demographers followed by population ecologists. If we know the vital rates of any population we can calculate its growth trajectory. We do not need to talk in qualitative terms because we have quantitative methods for population arithmetic (Caswell 2001; Ranta *et al.* 2006). The importance of population mathematics cannot be overemphasized because science is quantitative, and with quantitative methods you can find out when your empirical results are quantitatively incorrect and then begin to ask why.

Statistical methods

Closely aligned with population mathematics has been the development of statistical methods specific for population ecology. Statistical estimation theory, typified by Program MARK (Cooch & White 2010) and Program DENSITY (Efford *et al.* 2009) has brought new rigor to asking specific questions about survival and dispersal in marked populations. Statistical inference theory has dramatically improved our ability to apply strong inference to population processes (Anderson 2008), and Bayesian inference has provided new approaches to data evaluation and estimation (Ellison 1996; Hobbs & Hilborn 2006). While arguments have raged about the utility and misuse of *P*-values in ecol-

ogy (Anderson *et al.* 2000; Ioannidis 2005), no one seriously questions the value statistical methods have added to ecological research.

Experimental approaches

Population ecologists began to implement field experiments in the 1950s, and the value of experiments has been recognized ever since. This revolution was closely tied to discussion in the scientific world about how to make rapid progress in science and a general review of the best approaches to scientific inference (Platt 1964; Hilborn & Stearns 1982; Beck 1997). The key to much of this discussion is the underlying need for rigorous hypotheses with clear testable predictions that are relevant to the question at hand, along with alternative hypotheses with non-overlapping predictions (Anderson *et al.* 2000). An important qualification is that “experimental approaches” must not be confined to manipulative experiments, because the same approaches can be used for natural experiments and for systems that can only be observed, not manipulated (Diamond 1986). The recognition that most ecological systems are open systems has made the transfer of predictions made from closed systems difficult to evaluate (Oreskes 1998). For this reason many of the model system studies in population ecology were initially misleading.

Applied ecology

From a practical point of view the achievements of population ecologists working in applied areas are stellar. Not only do they help to solve practical problems of our society but they also provide an operational test of ecological theory. Consider marine fisheries management. Nearly 100 years ago fishery ecologists began to ask questions about optimal yield in marine fisheries (Graham 1935; Walters & Martell 2004). From this early start when marine fisheries were underexploited to the present day when many fisheries are fully exploited and some overexploited, a series of developments springing from population arithmetic have aided management and provided guidance for sustainable fisheries production (Hilborn 2007; Hauser & Carvalho 2008; Costello *et al.* 2012; Hilborn 2012).

Wildlife management has been a second important area in which population ecology and harvesting theory have worked together to produce sustainable hunting as well as improving freshwater fishing. Changes in wildlife populations caused by the elimination or reduction of major predators have been implicated in a series of problems with overabundant wildlife (Letnic & Koch 2010; Estes *et al.* 2011; Newsome & Ripple 2014; Rip-

ple *et al.* 2014). The result for wildlife management is that we know for the most part what population policies ought to be implemented for sustainable management, but in some situations political or social demands prevent their implementation. The same problem affects fisheries management. The ecology is sound but not always acceptable socially or politically.

Conservation biology is a third critical area in which population ecology in cooperation with conservation genetics has been able to produce practical recommendations for protecting threatened and endangered species. Early accomplishments in conservation biology were successful because they focused on individual species and their interactions, and for many of the species of concern there were detailed natural history and population data available. More recent conservation work has focused on communities and ecosystems, particularly in the era of climate change. Conservation biology operates with two well recognized paradigms defined by Graeme Caughley (Caughley 1994): the declining population paradigm and the small population paradigm. It is an action-oriented subdiscipline and its recommendations come from our accumulated ecological knowledge. That conservation actions may not always succeed is sometimes the result of ecologists diagnosing the problem incorrectly but perhaps more often the failure of social pressures and political policies that are difficult to change.

FAILURES IN POPULATION ECOLOGY

We ecologists should not ignore the failures of the past lest we repeat them, and I would like to summarize briefly the main problems that have affected population ecology particularly in the past 50 years. Four factors stand out.

The first has been the failure to state clear hypotheses and alternative hypotheses, along with the predictions each entails. The excuse for this is typically that we do not know enough to state clear hypotheses about the population under study. A simple example of this is the hypothesis that “the abundance of population X is limited by food supplies.” There are many observations we can make that are consistent with this hypothesis (e.g. “species X eats food Y which is relatively rare in the habitat”). The key is to state the observations that are not consistent with this hypothesis but are consistent with one of the alternative hypotheses. This is the method of strong inference presented by Chamberlin (Chamberlin 1897) and emphasized by Platt (1964). There are still too many hypotheses in population ecol-

ogy for which clear empirical tests have not been specified.

Figure 1 illustrates this problem with respect to the testing of model predictions. It does not matter for this illustration whether the predictions come from a verbal model or a strict mathematical model. Figure 1a illustrates the general dilemma in any science when exceptions are noted to predictions. One has to choose whether to abandon the hypothesis and develop another or whether to tinker with the hypothesis by restricting its range of application and, thereby, saving the hypothesis. Figure 1b gives a simple example from population growth theory. If the logistic equation does not describe the growth of a particular set of populations, we can modify the logistic model by restricting it to certain classes of populations, or we can abandon the model and find a better one. Kingsland (2005) discusses this logistic example in more detail and Caswell (2001) describes why matrix models are a better approach for this particular problem.

The second general failure in population ecology has been controversies over topics that lead nowhere. Reductionism versus holism is one philosophical example; density-dependence is another example from ecology. One possible solution that can help to stop these kinds of wasteful controversies is to ask the question: What practical problems can be answered by this topic? Peters (1991) suggests a similar question: What predictions follow from this topic? Density-dependence has always been a difficult issue, beloved of ecological modelers, distrusted by many field ecologists, an issue similar to competition and niche overlap in community ecology. There is (in my opinion) little point in arguing about points that do not connect directly to measurable items in the real world. Density-dependence in reproductive or mortality rates can be tested for in any population with enough data, but such results do not lead anywhere until the ecological mechanisms behind the relationships are understood.

A third general failure in population ecology has been the focus on short-term studies, typically demanded by universities of PhD dissertations and by the government research agencies who often assume that every problem can be solved in a 3-year research grant. A correlate of this issue has been a continued lack of appreciation of the need for monitoring. This general failure is now rapidly disappearing, and the issue of climate change has forced ecologists to think much more of long-term studies and long-term monitoring (Lindenmayer & Likens 2010; Lindenmayer *et al.* 2012). Short-term studies have the additional disadvantage of being confounded by transient events, and, thus, to reach conclusions

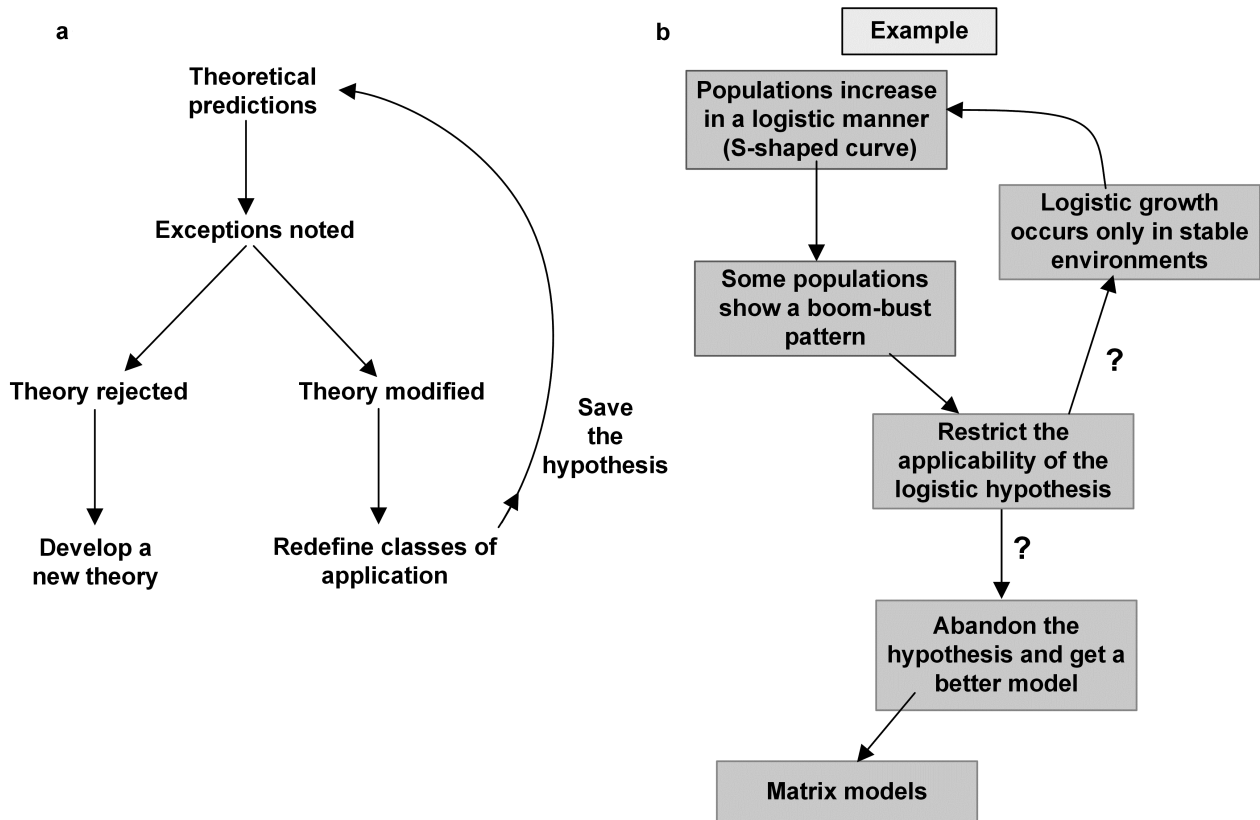


Figure 1 (a) A general diagram of the scientific method and possible ways of dealing with contrary results in any science. (b) One example from population ecology to illustrate how ecologists reacted to discovering that the logistic equation population growth model fits very few field data. Question marks indicate that one has to decide whether to continue to modify the logistic model (e.g. the theta-logistic) (Clark *et al.* 2010) or abandon it for a more general model of population change such as matrix models (Caswell 2001).

that are unreliable and cannot be extrapolated in space or time. The simple message is that more replication is needed.

A fourth common issue in ecology has been the failure to appreciate the assumptions behind statistical analyses. In spite of the publication of many excellent statistical texts we continually see tests of inference applied incorrectly because of the violation of assumptions. Many papers are full of statistical tests about hypotheses that every ecologist accepted long ago. Elegant AIC (Akaike information criterion) analysis tables are sometimes presented to test trivial points, simultaneously avoiding the difficult and important questions that do need testing. Graphs continually appear in all our journals with no error bars, no indication of the units of measurement, and no appreciation of how large an ef-

fect is produced by the different factors under study. All these failings can be brushed aside as minor details of little importance but in ecology more than ever we need clear thinking and clear presentations of results.

KEY ISSUES FOR FUTURE RESEARCH

One of the main goals for population ecology in the coming decade is to integrate its findings into community and ecosystem ecology. I will argue that you cannot conduct community and ecosystem studies without a firm foundation of the population ecology of the dominant species. Many ecologists disagree with this statement and yet the past is not a good guide for success of this contrary view. In the 1950s we thought we could reduce all of ecology to energy flow, so that species names

would become insignificant and knowing that they were herbivores or carnivores and how many calories they contained was enough to achieve ecological understanding. The difficulty was that many communities and ecosystems differ because of their evolutionary history, and general models of community and ecosystem function typically fail because they ignore the details of species interactions. Current attempts to use functional types are falling into the same trap of assuming some communality while ignoring evolutionary history (Ratnam *et al.* 2011; Boulangeat *et al.* 2012). These attempts are worth continuing only if we can get beyond the range of R^2 values > 0.5 .

There is no harm in trying to integrate community ecology with population dynamics by ignoring the species' peculiar traits, and this research is important to attempt. However, the most useful model that is now apparent is the food web approach (Memmott 2009; Thompson *et al.* 2012). There are an array of relatively new methods now available for linking food webs with the details of population ecology into the issues of communities and ecosystems. The key is to produce testable food web models with clear mechanistic relationships that flow from understanding population ecology (Thompson *et al.* 2012). New methods of network analysis integrated with food web studies present opportunities for advancement in our predictive understanding of ecosystem and community changes (Olf *et al.* 2009).

Many other key issues can be brought under the need to integrate populations and communities. Invasive species are a major problem all over the Earth, and population ecologists have had relatively poor success in predicting which species are likely to be invasive in spite of much research (Jeschke *et al.* 2012). Reducing the impacts of invasive species is another important focus of research that has been less successful than would be desired, perhaps because of the need to put invasive species into a clear community and ecosystem context (Norbury *et al.* 2013). Disease is another critical focus, and the spread of tropical diseases into temperate countries with climate change is a strong alarm call for more interaction in understanding the nexus of interactions that lead to disease transmission in plants and animals (Ostfeld *et al.* 2010; Xu *et al.* 2011).

Behind all of these issues is the larger long-term issue of how much ecological interactions can change due to evolutionary changes. Do population ecologists need to worry about microevolution while they juggle all these other factors we discussed previously? The simple answer now is that we do not know how many ecological interactions are fostering genetic changes in the short

timeframe of approximately 100 years. That we cannot dismiss these evo-eco issues is clear from our human interactions with growing resistance to pathogenic bacteria and viruses (Andersson & Hughes 2011), similarly increasing resistance to rodenticides in rats (Buckle 2013) and the problems of herbicide-resistant weeds (Shaner 2014). Ecology and evolution are inextricably tied together and we cannot use the excuse that this makes problems even more complex as a good reason for ignoring evolutionary changes in ecological interactions. However, the timeframe of evolutionary change in higher organisms may not mesh well with the timeframe of PhD dissertation and government research grants. We need to think of studies that will span the 50 to 100 year timeframe both to capture possible evolutionary changes and to monitor long-term slow ecological shifts, a difficult issue that is rarely discussed.

If the larger issues that face us as population ecologists have been outlined, we must not forget there are many components of what we do know that must be studied further to discover the gaps that are still unexplored. While we recognize landscape ecology as critical for understanding population dynamics, it is even more critical for community and ecosystem dynamics. Yet the resources needed for landscape ecology are rarely available in spite of this need. If we are unsure now of how much generality we can expect to find in population dynamics, we will need much further replication of our experiments in many locations to be able to answer this question (Borer *et al.* 2014). In general, we face all the same issues as other sciences in this regard. While molecular biology is currently the queen of the biological sciences, we recognize that even these scientists with all their resources have barely begun to put together the genetic patterns of life on Earth. We must continue to monitor, measure and experiment before we can achieve a synthesis of population, community and ecosystem ecology.

ACKNOWLEDGMENTS

I thank my colleagues for their insights into these issues, but I respect their differences of opinion on many of the questions raised here. In particular, I thank Judy Myers, Tony Sinclair, Rudy Boonstra, Stan Boutin, Zhibin Zhang and Jim Hone for sharing their thoughts about the future of ecological science. This research was supported by the Natural Sciences and Engineering Research Council of Canada and the Institute for Applied Ecology, University of Canberra.

REFERENCES

- Anderson DR (2008). *Model Based Inference in the Life Sciences: A Primer on Evidence*. Springer, New York.
- Anderson DR, Burnham KP, Thompson WL (2000). Null hypothesis testing: Problems, prevalence, and an alternative. *Journal of Wildlife Management* **64**, 912–23.
- Andersson DI, Hughes D (2011). Persistence of antibiotic resistance in bacterial populations. *FEMS Microbiology Reviews* **35**, 901–11.
- Andrewartha HG, Birch LC (1954). *The Distribution and Abundance of Animals*. University of Chicago Press, Chicago.
- Beck MW (1997). Inference and generality in ecology: Current problems and an experimental solution. *Oikos* **78**, 265–73.
- Borer ET, Harpole WS, Adler PB *et al.* (2014). Finding generality in ecology: A model for globally distributed experiments. *Methods in Ecology and Evolution* **5**, 65–73.
- Boulangeat I, Philippe P, Abdulhak S *et al.* (2012). Improving plant functional groups for dynamic models of biodiversity: At the crossroads between functional and community ecology. *Global Change Biology* **18**, 3464–75.
- Buckle A (2013). Anticoagulant resistance in the United Kingdom and a new guideline for the management of resistant infestations of Norway rats (*Rattus norvegicus* Berk.). *Pest Management Science* **69**, 334–41.
- Caswell H (2001). *Matrix Population Models: Construction, Analysis, and Interpretation*, 2nd edn. Sinauer Associates, Sunderland, MA.
- Caughley G (1994). Directions in conservation biology. *Journal of Animal Ecology* **63**, 215–44.
- Chamberlin TC (1897). The method of multiple working hypotheses. *Journal of Geology* **5**, 837–48 (reprinted in *Science* **148**: 754–59 in 1965).
- Chitty D (1996). *Do Lemmings Commit Suicide? Beautiful Hypotheses and Ugly Facts*. Oxford University Press, New York.
- Clark F, Brook BW, Delean S, Reşit Akçakaya H, Bradshaw CJA (2010). The theta-logistic is unreliable for modelling most census data. *Methods in Ecology and Evolution* **1**, 253–62.
- Cooch E, White GC (2010). *Program MARK: A Gentle Introduction*, 9th edn. <http://www.phidot.org/software/mark/docs/book/>.
- Costello C, Ovando D, Hilborn R, Gaines SD, De-schenes O, Lester SE (2012). Status and solutions for the world's unassessed fisheries. *Science* **338**, 517–20.
- Crowcroft P (1991). *Elton's Ecologists: A History of the Bureau of Animal Population*. University of Chicago Press, Chicago.
- Diamond J (1986). Overview: Laboratory experiments, field experiments, and natural experiments. In: Diamond J, Case TJ, eds. *Community Ecology*. Harper and Row, New York, pp. 3–22.
- Efford MG, Borchers DL, Byrom AE (2009). Density estimation by spatially explicit capture-recapture: likelihood-based methods. In: Thomson DL, Cooch EG, Conroy MJ, eds. *Modeling Demographic Processes in Marked Populations*. Springer, New York, pp. 255–69.
- Ellison AM (1996). An introduction to Bayesian inference for ecological research and environmental decision-making. *Ecological Applications* **6**, 1036–46.
- Elton C (1927). *Animal Ecology*. Sidgwick and Jackson, London.
- Estes JA, Terborgh J, Brashares JS *et al.* (2011). Trophic downgrading of Planet Earth. *Science* **333**, 301–6.
- Ginzburg LR, Jensen CXJ, Yule JV (2007). Aiming the “unreasonable effectiveness of mathematics” at ecological theory. *Ecological Modelling* **207**, 356–62.
- Graham M (1935). Modern theory of exploiting a fishery, and application to North Sea trawling. *Journal du Conseil Permanente International pour l'Exploration de la Mer* **10**, 264–74.
- Graham MH, Dayton PK (2002). On the evolution of ecological ideas: Paradigms and scientific progress. *Ecology* **83**, 1481–9.
- Hauser L, Carvalho GR (2008). Paradigm shifts in marine fisheries genetics: Ugly hypotheses slain by beautiful facts. *Fish & Fisheries* **9**, 333–42.
- Hilborn R (2007). Defining success in fisheries and conflicts in objectives. *Marine Policy* **31**, 153–8.
- Hilborn R (2012). The evolution of quantitative marine fisheries management 1985–2010. *Natural Resource Modeling* **25**, 122–44.
- Hilborn R, Stearns SC (1982). On inference in ecology and evolutionary biology: The problem of multiple causes. *Acta Biotheoretica* **31**, 145–64.
- Hobbs NT, Hilborn R (2006). Alternatives to statistical hypothesis testing in ecology: A guide to self teaching. *Ecological Applications* **16**, 5–19.
- Ioannidis JPA (2005). Why most published research findings are false. *PLoS Medicine* **2**, e124.

- Jeschke J, Gómez Aparicio L, Haider S *et al.* (2012). Support for major hypotheses in invasion biology is uneven and declining. *NeoBiota* **14**, 1–20.
- Kershaw HM, Mallik AU (2013). Predicting plant diversity response to disturbance: Applicability of the intermediate disturbance hypothesis and mass ratio hypothesis. *Critical Reviews in Plant Sciences* **32**, 383–95.
- Kingsland SE (2005). *The Evolution of American Ecology, 1890-2000*. Johns Hopkins University Press, Baltimore.
- Lawton J (1991). Predictable plots. *Nature* **354**, 444.
- Letnic M, Koch F (2010). Are dingoes a trophic regulator in arid Australia? A comparison of mammal communities on either side of the dingo fence. *Austral Ecology* **35**, 167–75.
- Lidicker WZ Jr (1995). The landscape concept: Something old, something new. In: Lidicker WZ Jr, ed. *Landscape Approaches in Mammalian Ecology and Conservation*. University of Minnesota Press, Minneapolis, pp. 3–19.
- Lindenmayer DB, Likens GE (2010). *Effective Ecological Monitoring CSIRO Press*. Collingwood, Victoria.
- Lindenmayer DB, Likens GE, Andersen A *et al.* (2012). Value of long-term ecological studies. *Austral Ecology* **37**, 745–57.
- McIntosh RP (1985). *The Background of Ecology: Concept and Theory*. Cambridge University Press, Cambridge.
- Memmott J (2009). Food webs: A ladder for picking strawberries or a practical tool for practical problems? *Philosophical Transactions of the Royal Society B* **364**, 1693–9.
- Newsome TM, Ripple WJ (2014). A continental scale trophic cascade from wolves through coyotes to foxes. *Journal of Animal Ecology* **84**, 49–59.
- Norbury G, Byrom A, Pech R *et al.* (2013). Invasive mammals and habitat modification interact to generate unforeseen outcomes for indigenous fauna. *Ecological Applications* **23**, 1707–21.
- O'Connor RJ (2000). Why ecology lags behind biology. *The Scientist* **14**, 35.
- Olf H, Alonso D, Berg MP *et al.* (2009). Parallel ecological networks in ecosystems. *Philosophical Transactions of the Royal Society B* **364**, 1755–79.
- Oreskes N (1998). Evaluation (not validation) of quantitative models. *Environmental Health Perspectives Supplements* **106**, 1453–60.
- Ostfeld RS, Keesing F, Eviner VT, eds (2010). *Infectious Disease Ecology: Effects of Ecosystems on Disease and of Disease on Ecosystems*. Princeton University Press, Princeton, New Jersey.
- Peters RH (1991). *A Critique for Ecology*. Cambridge University Press, Cambridge, UK.
- Platt JR (1964). Strong inference. *Science* **146**, 347–53.
- Ranta E, Lundberg P, Kaitala V (2006). *Ecology of Populations*. Cambridge University Press, Cambridge, MA.
- Ratnam J, Bond WJ, Fensham RJ *et al.* (2011). When is a 'forest' a savanna, and why does it matter? *Global Ecology and Biogeography* **20**, 653–60.
- Ripple WJ, Beschta RL, Fortin JK, Robbins CT (2014). Trophic cascades from wolves to grizzly bears in Yellowstone. *Journal of Animal Ecology* **83**, 223–33.
- Shaner DL (2014). Lessons learned from the history of herbicide resistance. *Weed Science* **62**, 427–31.
- Strong DR (1986). Density-vague population change. *Trends in Ecology and Evolution* **1**, 39–42.
- Thompson RM, Brose U, Dunne JA *et al.* (2012). Food webs: Reconciling the structure and function of biodiversity. *Trends in Ecology & Evolution* **27**, 689–97.
- Uyeda S (2013). On earthquake prediction in Japan. *Proceedings of the Japan Academy, Series B* **89**, 391–400.
- Walters CJ, Martell SJD (2004). *Fisheries Ecology and Management*. Princeton University Press, Princeton, New Jersey.
- Wolff JO, Sherman PW, eds (2007). *Rodent Societies: An Ecological and Evolutionary Perspective*. University of Chicago Press Chicago.
- Xu L, Liu Q, Stige LC *et al.* (2011). Nonlinear effect of climate on plague during the third pandemic in China. *PNAS* **108**, 10214–9.

Cite this article as:

Krebs C (2015). One hundred years of population ecology: Successes, failures and the road ahead. *Integrative Zoology* **10**, 233–40.