



Aligning science and policy to achieve evolutionarily enlightened conservation

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Abstract: *There is increasing recognition among conservation scientists that long-term conservation outcomes could be improved through better integration of evolutionary theory into management practices. Despite concerns that the importance of key concepts emerging from evolutionary theory (i.e., evolutionary principles and processes) are not being recognized by managers, there has been little effort to determine the level of integration of evolutionary theory into conservation policy and practice. We assessed conservation policy at 3 scales (international, national, and provincial) on 3 continents to quantify the degree to which key evolutionary concepts, such as genetic diversity and gene flow, are being incorporated into conservation practice. We also evaluated the availability of clear guidance within the applied evolutionary biology literature as to how managers can change their management practices to achieve better conservation outcomes. Despite widespread recognition of the importance of maintaining genetic diversity, conservation policies provide little guidance about how this can be achieved in practice and other relevant evolutionary concepts, such as inbreeding depression, are mentioned rarely. In some cases the poor integration of evolutionary concepts into management reflects a lack of decision-support tools in the literature. Where these tools are available, such as risk-assessment frameworks, they are not being adopted by conservation policy makers, suggesting that the availability of a strong evidence base is not the only barrier to evolutionarily enlightened management. We believe there is a clear need for more engagement by evolutionary biologists with policy makers to develop practical guidelines that will help managers make changes to conservation practice. There is also an urgent need for more research to better understand the barriers to and opportunities for incorporating evolutionary theory into conservation practice.*

Keywords: adaptive potential, conservation policy, evolution, evolutionary resilience, genetic diversity, genetic management

Alinear a la Ciencia y a la Política para Alcanzar la Conservación Informada Evolutivamente

Resumen: *Hay un reconocimiento creciente entre los científicos de la conservación de que los resultados a largo plazo de la conservación podrían mejorarse por medio de una mejor integración de la teoría evolutiva dentro de las prácticas de manejo. A pesar de la preocupación que genera que la importancia de los conceptos claves emergentes de la teoría evolutiva (es decir, procesos y principios evolutivos) no es reconocida por los administradores, ha habido muy pocos esfuerzos para determinar el nivel de integración de la teoría evolutiva dentro de la práctica y la política de la conservación. Valoramos la política de conservación a tres escalas (internacional, nacional y provincial) en tres continentes para cuantificar el grado en el que los conceptos evolutivos importantes, como la diversidad genética y el flujo génico, están siendo incorporados a la práctica de la conservación. También evaluamos la disponibilidad de una guía clara dentro de la aplicación de la literatura sobre la biología evolutiva de cómo los administradores pueden cambiar sus prácticas de manejo para obtener mejores resultados de conservación. A pesar del reconocimiento extenso de la importancia de mantener la diversidad genética, las políticas de conservación proporcionan poca dirección sobre cómo puede obtenerse esto en la práctica y otros conceptos evolutivos, como la depresión endogámica, son mencionados raramente. En algunos casos la reducida integración de los conceptos evolutivos dentro del manejo, refleja una falta de herramientas de apoyo para las decisiones en la literatura. En donde esas herramientas están disponibles, como en los marcos de trabajo de valoración de riesgos, no están siendo adoptadas por quienes*

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hacen las políticas de conservación, lo que sugiere que la disponibilidad de una base de evidencias fuertes no es la única barrera para el manejo informado evolutivamente. Creemos que se requiere una mayor participación por parte de los biólogos evolutivos con quienes hacen las políticas para desarrollar pautas prácticas que ayudarán a los administradores a realizar cambios a la práctica de la conservación. También existe es urgente realizar más investigación para entender de mejor manera las barreras y las oportunidades para incorporar a la teoría evolutiva dentro de la práctica de la conservación.

Palabras Clave: diversidad genética, evolución, manejo genético, política de conservación, potencial adaptativo, resiliencia evolutiva

Introduction

Despite being part of the original framing of conservation biology as a discipline (Soulé 1985), evolutionary biology has received less attention than ecology in conservation (Smith et al. 2014). The crisis-discipline mentality of conservation science has contributed to a focus on immediate actions to conserve species and communities. Achieving the long-term persistence of species has been a secondary objective, and short-term goals, such as maintaining critically endangered species, are the focus of decision making (Frankham 2010). Increasing environmental change emphasizes the importance of maintaining ecological and evolutionary processes so that populations can adapt to climate change (Hoffmann & Sgrò 2011; Sgrò et al. 2011). Despite the value of applying evolutionary concepts (evolutionary processes and principles derived from evolutionary theory and population genetics) to achieve better long-term conservation outcomes, these ideas are rarely incorporated in practice (Mace & Purvis 2008; Smith et al. 2014).

Evolutionary biology is not alone in facing challenges in translating theory into conservation practice. The evidence-based conservation movement (Dicks et al. 2014) provides an excellent foundation with which to assess the current integration of evolutionary concepts into conservation. It is increasingly recognized that for science to be translated into practice it must address management-relevant questions (e.g., Fazey et al. 2005), provide decision-support tools (e.g., Cook et al. 2016), and be coupled with active engagement between scientists and managers (Cook et al. 2013). Unfortunately, research into the translation of evolutionary biology into conservation practice is still in its infancy; there is little more than anecdotal evidence of the uptake of theory (Smith et al. 2014; Ridley & Alexander 2016). Finding effective ways to improve integration of evolutionary concepts requires understanding current penetration of evolutionary concepts in conservation policy and practice; availability of research demonstrating the benefits of changing management practices; and guidance and tools available to improve management activities. The inability to answer these questions is a significant barrier to achieving better conservation outcomes.

A precursor to changing on-the-ground practices is to modify conservation policy. Therefore, knowing the current status of evolutionary concepts within conservation policy is critical for determining how to increase the long-term effectiveness of conservation. Despite growing criticism (Lankau et al. 2011; Smith et al. 2014), there has been little effort to evaluate the adoption of evolutionary concepts into conservation policy (Santamaria & Mendez 2012; Hoban et al. 2013). One key message from evolutionary biologists has been the importance of managing populations to maintain genetic diversity (GD) (Sgró et al. 2011; Weeks et al. 2011). There is evidence that this message has been heeded by policy makers; international conservation policy recognizes that GD is a critical element of biodiversity and human well-being (Santamaria & Mendez 2012). The Convention on Biological Diversity (CBD) and the Millennium Ecosystem Assessment (MA) explicitly mention the importance of GD. The CBD (2010) sets targets that explicitly call for GD to be actively conserved (e.g., Aichi Target 13). However, this awareness has not translated into proposed actions, indicators of progress, or programs to monitor GD (Laikre et al. 2010). Beyond mentioning GD, there has been little assessment of the integration of evolutionary concepts into conservation policy.

To understand the extent to which relevant concepts from evolutionary theory are being integrated into conservation, we assessed the incorporation of key concepts into conservation policy at international, national, and provincial levels. We also assessed the availability of guidance and decision-support tools to assist with the integration of these concepts into policy and practice. By advancing understanding of the level of integration of evolutionary theory into conservation policy and practice and relating this to the development of management-relevant science to operationalize relevant theory, it may be possible to apply evolutionary theory for successful long-term conservation.

Methods

Study System

To generate an in-depth assessment of the degree to which concepts from evolutionary biology have been integrated into conservation policy, we analyzed

Table 1. Key concepts relevant to integrating evolutionary principles and processes into conservation practice.

<i>Evolutionary concept</i>	<i>Definition</i>	<i>Relevant policy areas</i>
General		
genetic diversity	genetic differences between individuals of the same species	threatened species, restoration and revegetation, invasive species, protected areas
adaptation*	condition where the phenotype of individuals are well suited to the environmental conditions, such that the individuals have higher reproductive fitness	threatened species, restoration and revegetation, invasive species, protected areas
evolution	process by which populations or species change over successive generations	threatened species, restoration and revegetation, invasive species, protected areas
Specific		
gene flow	movement of alleles between populations through mating between individuals from different populations	threatened species, restoration and revegetation, invasive species, protected areas
inbreeding depression	mating between closely related individuals that leads to a loss of genetic diversity and corresponding reduction in reproductive fitness	threatened species, restoration and revegetation
outbreeding depression	mating between genetically distinct individuals that introduces new alleles that disrupt local adaptation and lead to reduced reproductive fitness	threatened species, restoration and revegetation
mating system	way in which a population is structured in relation to sexual behavior	threatened species, invasive species
life history strategy	way in which individuals invest in growth, reproduction, and survival	threatened species, invasive species

*We excluded references to adaptation when the word was used in relation to strategies or actions conducted in response to changing social or environmental conditions.

policy documents at international, national, and provincial scales. At the international scale, agreed-upon commitments, targets, and objectives centered on influencing policy (e.g., CBD) can influence signatory countries.

At the national scale, we focused on Australia, Canada, and South Africa. Each country has large, diverse geographic areas covering a wide range of environments (e.g., tropical, temperate, arid) and complex environmental governance arrangements under which both national and provincial governments are responsible for conservation.

The diversity of environments and their distribution across 8 Australian, 9 South African, and 13 Canadian provincial jurisdictions (Supporting Information), all with their own governing policies and legislation, provides an excellent opportunity to compare policy environments.

Literature Compilation

We conducted targeted searches for policy and legislative documents relevant to biodiversity conservation, including general conservation policies (e.g., biodiversity strategies, climate-change strategies) and conservation policies relevant to specific aspects of management (i.e., threatened species, invasive species, habitat restoration, and protected areas) mentioned in the applied evolution literature as likely to benefit from greater integration of evolutionary theory (see “Content Analyses”).

We identified policies from official websites of relevant international bodies and government agencies. International policy documents were sourced from the CBD, International Union for the Conservation of Nature (IUCN), MA, and the United Nation’s Sustainable Development Goals.

To estimate the volume of peer-reviewed literature on the relevance of key general and specific evolutionary concepts to conservation (Table 1), we conducted targeted searches through Web of Science for the search terms conservation and evolution, adaptation, genetic diversity, gene flow, inbreeding depression, outbreeding depression, mating system, and life history. These searches were restricted to the conservation literature and excluded the fields of medicine, biotechnology, engineering, fisheries, forestry, and agriculture.

To identify studies with practical application to conservation, we used 7 recent reviews to identify relevant literature (i.e., Mace & Purvis 2008; Hoffmann & Sgrò 2011; Lankau et al. 2011; Sgrò et al. 2011; Weeks et al. 2011; Carroll et al. 2014; Smith et al. 2014). We then used a snowballing approach to search the reference list of relevant publications to identify additional relevant studies. All literature relevant to conservation were captured in this search, including studies from natural resource management. We searched for articles that discuss the integration of evolutionary concepts into management; provide

Table 2. The number of relevant policy documents included in the content analysis for each jurisdiction.^a

Jurisdiction	Number of general policy documents	Number of specific policy documents				Total ^b
		threatened species and ecosystems	restoration or revegetation	invasive species	protected areas	
International	23	5	0	2	1	31
National						
Australia	16 (1)	2 (0)	4 (0)	3 (0)	2 (1)	29
Canada	3 (2)	6 (2)	2 (0)	1 (4)	2 (2)	21
South Africa	8 (2)	(1)	0 (0)	3 (0)	2 (4)	19
Provincial						
Australia (mean)	6.9 (1.5)	2.4 (1.0)	1.7 (0.4)	2.5 (0.5)	1.1 (1.8)	18.4
Canada (mean)	2.9 (2.2)	1.6 (1.1)	0.8 (0)	0.9 (1.2)	1.2 (2.5)	13.6
South Africa (mean)	2.2 (0.2)	0 (1.1)	0 (0)	0.1 (0.2)	0.3 (1)	4.1

^aNumbers in parentheses indicate pieces of legislation.

^bRow numbers do not sum to the total because some policy documents and legislation span multiple categories.

empirical evidence for the effectiveness of altered management practices in a conservation context; and present or describe decision-support tools practitioners could use to translate relevant concepts into management action.

For all papers we recorded discussion of the policy areas that could benefit from integrating evolutionary concepts; practical advice on how to change management practices; and case studies that demonstrated the conservation benefits of altered management.

Content Analyses

We used the software NVivo (version 10.0.4) (QSR International 2012) for our content analysis of the policy documents. All relevant documents were compiled in NVivo databases and searched for keywords or recurring themes (Patton 2002). We coded the documents depending on the research question. We used an inductive category-development method in which categories were not defined a priori but instead were developed based on common themes (i.e., open coding) or a deductive category-development method whereby categories were developed based on a priori hypotheses (Patton 2002).

Our hypothesis was that the uptake of evolutionary concepts within conservation practice is related to progress in the peer-reviewed literature translating theory into practical recommendations for action. Progress was defined as promising theoretical developments that require research on conservation application; empirical evidence from model organisms not yet translated into a management context; complex evidence generating debate about the risks and benefits of application; strong evidence with broad agreement on importance but not application; clear practical application with associated decision-support tools; or clear demonstration of the beneficial outcomes of changing management practices.

To assess the integration of evolution into conservation, we developed key evolutionary concepts (Table 1) suggested as important for designing effective manage-

ment actions. We selected these concepts based on our knowledge of the principles and processes commonly discussed in the evolutionary-applications literature and through discussions with other evolutionary biologists. We searched the policy documents for references to these key concepts (Table 1) and calculated the relative frequency of policy documents mentioning each concept. Because not all concepts were equally likely to be discussed in all types of policies, we calculated relative frequency based on the relevant policy areas (Table 1).

We searched the peer-reviewed literature for references to the aspects of management that could benefit from greater integration of evolutionary concepts. We used these management aspects to structure our search of the relevant policy areas.

To understand how relevant concepts were being discussed within policy documents, we classified the context in which the term genetic diversity was used within conservation policies. We recorded the aspects of conservation that GD was being described as relevant to and the level of detail associated with any recommendations (e.g., practical guidance for application to management decisions).

Quantitative Data Analyses

We used analysis of variance to compare the rates at which different evolutionary concepts were mentioned in policy documents at the national and at the provincial scale.

Results

Evolutionary Concepts in Conservation Policy and Science

We identified a wide range of general and specific policies and legislation relevant to biodiversity conservation at all levels (Table 2 & Supporting Information). Genetic diversity was mentioned significantly more often in

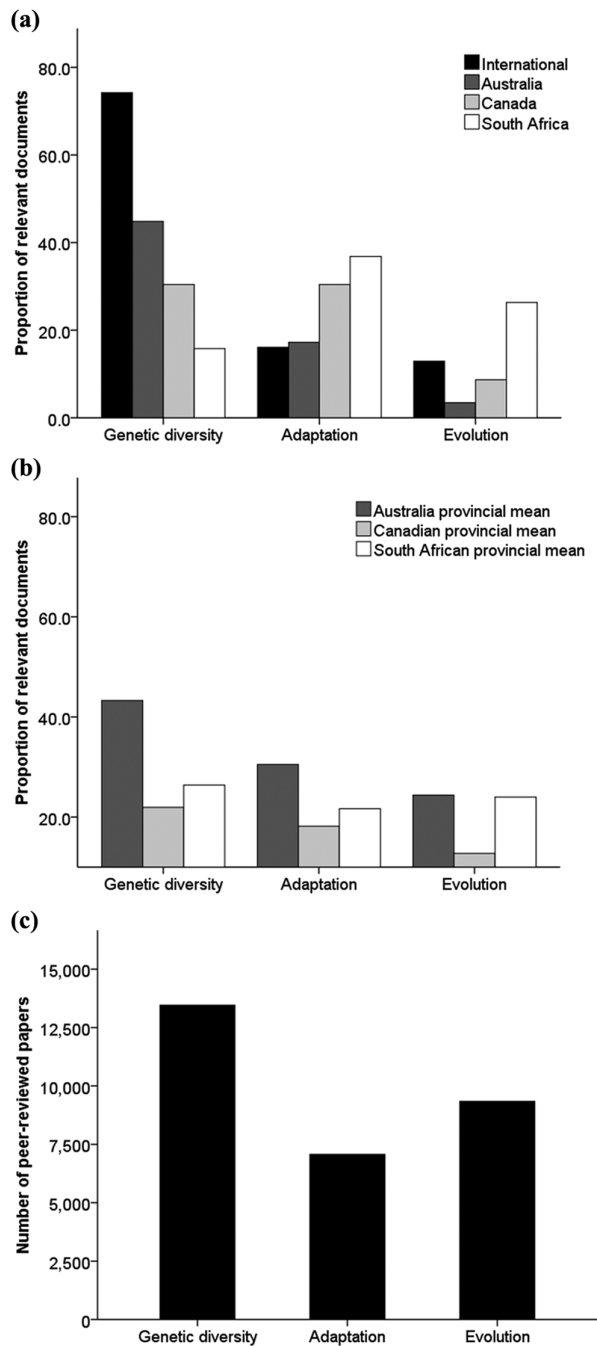


Figure 1. Frequency with which general evolutionary concepts relevant to conservation biology are mentioned in (a) international and national and (b) provincial conservation-policy documents and (c) number of peer-reviewed articles on these concepts in the conservation literature.

conservation policies than the other key evolutionary concepts (Table 1 & Fig. 1a & 3a) ($F_{1,7} = 5.57$, $p = 0.001$); this mirrored the trend in the conservation literature (Figs. 1c & 3c). The strongest emphasis on GD was in international policy documents, followed by Australian

policies (Fig. 1a). Canadian and South African policies tended to place slightly higher emphasis on adaptation than the other jurisdictions (Fig. 1a). At the provincial level, general evolutionary concepts (genetic diversity, adaptation, and evolution) were mentioned more often than other evolutionary concepts (Figs. 1b & 3b) ($F_{1,7} = 6.13$; $p < 0.001$). Despite a greater emphasis on GD, less than half the national and provincial policy documents mentioned GD in Australia, and even fewer documents mentioned GD in Canada and South Africa (Fig. 1a).

The discussion of evolution and adaptation within policy documents was far more limited, although South African and to some extent Canadian policies were more likely to mention these concepts than Australian or international documents (Fig. 1a). Nevertheless, Australian policies were more likely to discuss evolution or adaptation in relation to GD (Fig. 1). This link between the concepts was rarely observed in Canadian or South African policies (Fig. 1), in direct contrast with the peer-review literature (Fig. 1c).

Mention of GD tended to be generic (i.e., its importance to biodiversity and to threatened species management) (Fig. 2). Within Australian policies, GD was often included only within the definition of biodiversity, a pattern mirrored at the provincial level across all jurisdictions (Fig. 2). There was little discussion of the relevance of GD to conservation. International policies, and to a lesser extent South African national policies, tended to give greater emphasis to GD in relation to agriculture and food security (Fig. 2a). The focus on the importance of GD to ecosystem services often made reference to domesticated animals and cultivated plants as set out within the CBD (2010) (target 13). However, this pattern was not observed at the provincial scale; agriculture was rarely mentioned (Fig. 2b) because policies relating specifically to agriculture are generally covered in separate documents.

Although far less common, GD was mentioned in a range of more specific management contexts in policy documents (Fig. 2). South Africa tended to include GD in a much narrower range of contexts than Australia or Canada; GD was mentioned in the context of threatened species, agriculture, and invasive species (Fig. 2). Australian and Canadian policies included discussion of the value of genetic tools for determining species identity, especially where hybridization between species was a concern (Fig. 2). Genetic diversity was also discussed in relation to the long-term success of habitat restoration and the importance of connectivity and gene flow for maintaining GD (Fig. 2). A notable trend across all levels of conservation policy was the low level of recognition of GD for informing the management of invasive species. However, South African policies tended to give this slightly more emphasis than other jurisdictions (Fig. 2). In all cases, discussion of the relevance of GD to these aspects of conservation was broad (e.g., habitat fragmentation can lead to a loss of GD) without reference to specific

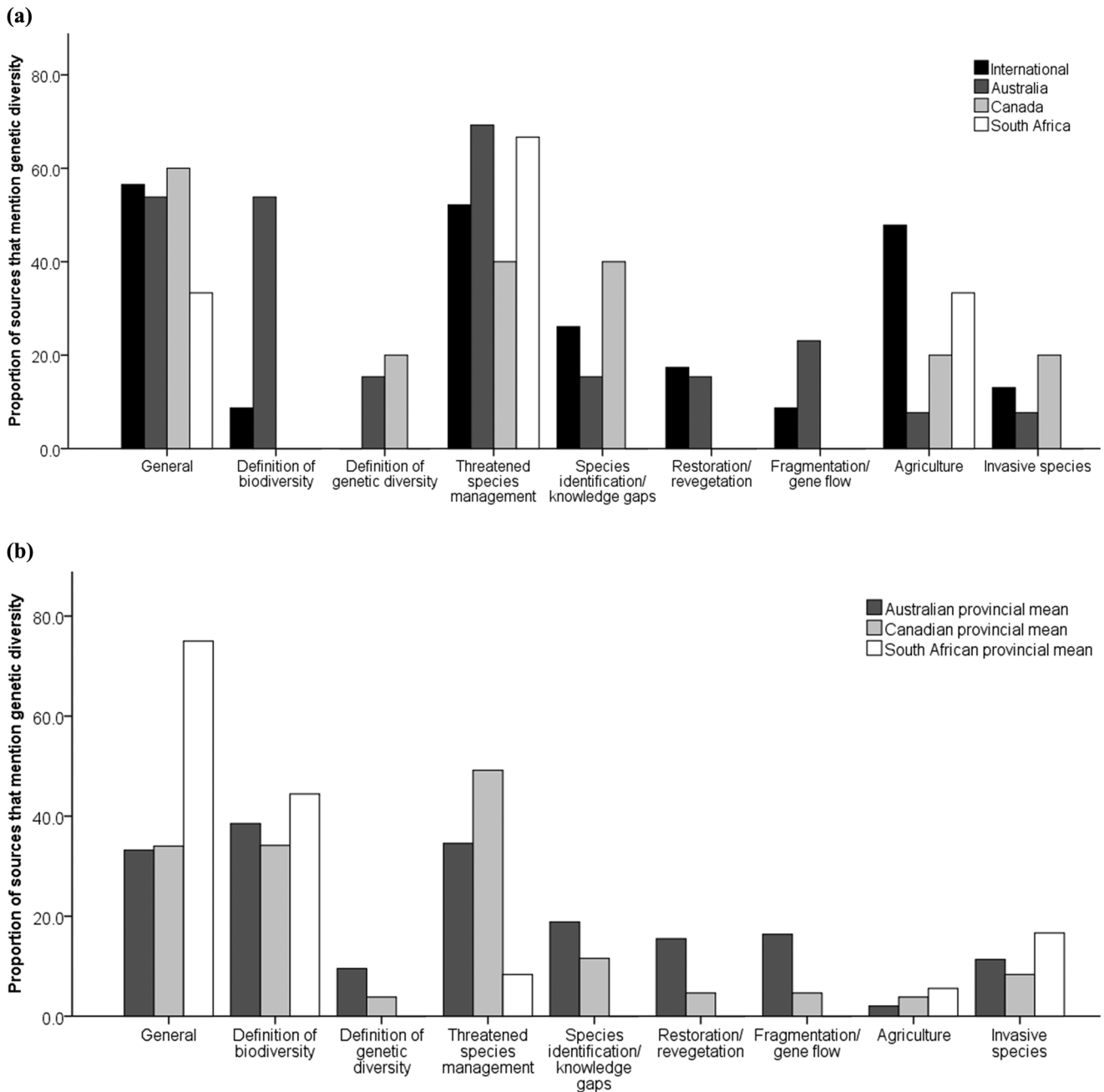


Figure 2. The context in which genetic diversity is mentioned in (a) international and national and (b) provincial policy documents.

management actions or to risk assessment and decision-support tools available in the literature (e.g., Table 3).

Specific Evolutionary Concepts in Conservation Policy

There was little mention of more specific evolutionary concepts within biodiversity policies (Fig. 3). International and Australian provinces were the only jurisdictions where all the concepts were mentioned in at least one policy (Fig. 3). The concepts of outbreeding depression and mating systems were particularly poorly

represented; documents from only 2 Australian provinces mentioned both concepts (Supporting Information). South African provincial policies discussed only gene flow (Fig. 3b). Relative to the other countries, Australian provinces stood out in the frequency with which their policies mentioned inbreeding depression, life-history strategies, and gene flow (Fig. 3b).

National policies were extremely limited in the evolutionary concepts they discussed; no country mentioned >3 specific evolutionary concepts across all their policy documents (Fig. 3a), suggesting leadership is not

Table 3. Areas with a sufficient evidence base to guide decision making.^a

Concept	Type of guidance	Examples of demonstrated success
Minimize outbreeding depression	decision tree and guidelines for managers (1,2) that supersede previous guidelines (3)	One hundred forty-five of 156 studies show beneficial effects; however, only 48 were field-based studies, whereas 108 were based on laboratory or greenhouse experiments of model organisms (1). Broadly demonstrated in the literature (e.g., 5).
Minimize inbreeding depression	Promote gene flow, but there is disagreement about how this should be achieved (4) (Table 4).	common garden experiment of 6 species (7)
Revegetation	decision tree for assessing the risk of negative impacts on surrounding native vegetation (6)	empirical evidence conflicting, demonstrating several factors should influence decisions about where to source seed (9)
Seed sourcing	decision framework (8) and general guidance with some management suggestion (9)	Steelhead trout raised in hatcheries for one generation show higher fitness than those raised for multiple generations (12).
Captive breeding	Provide general guidance to manage captive populations to maintain genetic diversity and minimize inbreeding depression. Reduce adaptation to captivity by minimizing the number of generations in captivity (when possible) and keeping multiple, small, isolated captive populations with occasional outcrossing (10,11).	Fragmenting captive populations of the Lake Victoria cichlid (<i>Haplochromis perrieri</i>) do not reduce heterozygosity after 5 generations (13).
Genetic rescue	framework for assessing the risks and benefits (14)	Florida panther, <i>Puma concolor coryi</i> (15) (Hedrick 1995); Mexican wolf, <i>Canis lupus baileyi</i> (3); Greater Prairie Chicken, <i>Tympanuchus cupido pinnatus</i> (16); button wrinklework, <i>Rudidosia leptorrhynchoides</i> (17)
Translocation	risk assessment for translocation under a range of conditions (14) and general guidance based on the significant predictors of successful plant reintroductions (18)	many examples in (14) and (18)
Herbicide and pesticide use	Application at low dosage rates can increase rates of resistance (19). Leave untreated areas as refuges for individuals with susceptible genotypes to reduce the frequency of resistance alleles (20).	annual ryegrass, <i>Lolium rigidum</i> (21) Evidence for effectiveness of refuges comes from insecticide resistance in transgenic crops (22).
Use of multiple biocontrol agents ^b	Multiple agents slow an exotic species' ability to adapt to the agent.	Meta-analysis shows addition of 2 or more agents increases mortality by 13% (23).
Prevent multiple invasions ^b	Multiple invasions can lead to increased genetic diversity that facilitates adaptation to new habitats (20).	ragweed, <i>Ambrosia artemisiifolia</i> (24); Scotch broome, <i>Cytisus scoparius</i> (25)
Corridors	Prioritize corridors across environmental gradients to facilitate climatic adaptation. Balance benefits to native populations with increased invasion potential for pests and disease (26).	many examples of species range shifts in response to changing climate (8)
Focus on environmental gradients (evolutionary refuges)	Genetic diversity along environmental gradients can provide a reservoir of adaptive potential (20).	method proposed to illustrate how phylogenetic and intrapopulation diversity can be mapped across landscapes (environmental gradients) to protect areas that facilitate ongoing climate adaptation (27)
Large, connected populations ^b	Large, connected populations contain higher levels of genetic diversity (28).	many examples cited in (28)

^aNumbers in parentheses refer to references provided in Supporting Information.

^bMay be unavailable to managers due to circumstances beyond their control.

top down. Within national policies, life-history strategies, inbreeding depression, and gene flow were mentioned, although in <20% of relevant policies (Fig. 3a).

At all levels, the discussion of the key evolutionary concepts (Table 1) was restricted to recognition of the relevance of these concepts and there were no references

to management actions. Concepts, such as life-history strategy, gene flow, and inbreeding depression, were more likely to be mentioned in policy documents relevant to threatened species management, but again these references were general rather than providing direction about how risks should be managed.

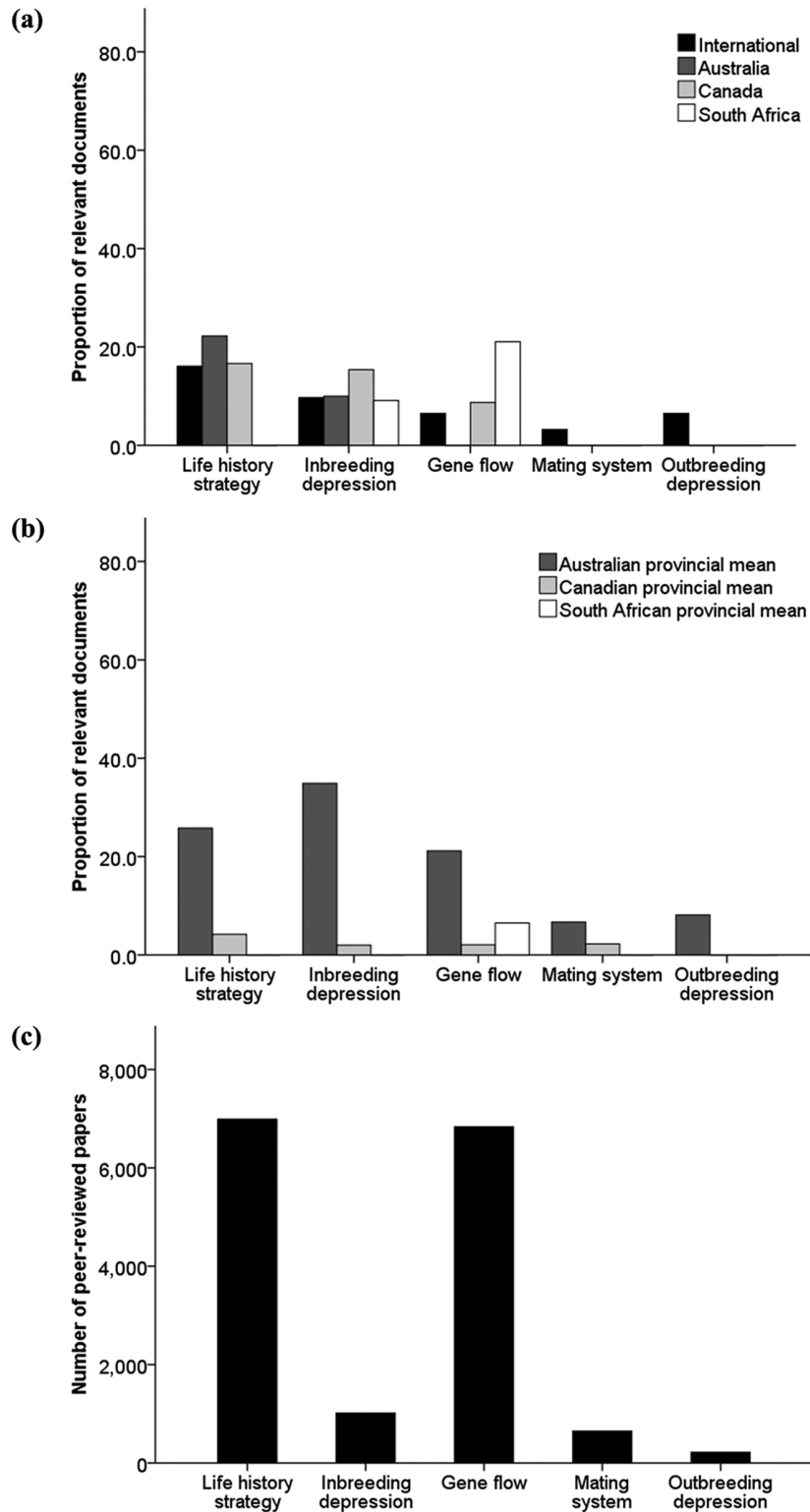


Figure 3. The frequency with which specific evolutionary concepts relevant to conservation are mentioned in (a) international and national and (b) provincial policy documents and (c) number of peer-reviewed articles on these concepts in the conservation literature.

Scientific Literature

There was a mismatch between the relative emphasis given to key evolutionary concepts in conservation policy and the literature (Figs. 1 & 3). Within the scientific literature, the discussion of general evolutionary concepts, such as GD, was common (Fig. 1c). The number of papers mentioning conservation and GD increased by 270% from 2005 to 2015 (result not shown). The relevance of life-history strategies and gene flow to population management was more commonly discussed in the literature than policies; however, inbreeding depression was given relatively greater emphasis in conservation policy than in the literature (Fig. 3). The importance of considering mating systems and outbreeding depression in decisions was infrequently discussed within both the conservation literature and policies (Fig. 3). We found evidence that many areas of evolutionary biology have a strong, empirical evidence base to support changing management practices, and there is general guidance available for many management issues within the evolutionary applications literature (Table 3).

Outbreeding depression was a notable aspect of the evolutionary applications literature, and it provided a sound evidence base (particularly for flora) and guidelines to help managers minimize the risk of outbreeding depression when moving individuals between populations (Table 3). These guidelines have been evaluated and provide strong evidence that outbreeding depression can be avoided (Table 3). Two other areas of the literature with a strong or growing evidence base for the benefits of changing management practices include sourcing seed for revegetation projects and gene-pool mixing (admixture) to purge deleterious alleles from populations suffering from inbreeding depression (i.e., genetic rescue) (Table 3).

In the scientific literature there is disagreement about the benefits of proposed changes to management (Table 4). Some debate arises from conflicting empirical evidence about the benefits of different management strategies. For example, gene flow can be highly beneficial in preserving GD and adaptive potential but may inhibit local adaptation (Table 4). Other debates center on the application of new technology (e.g., genetic monitoring) or superseded ideas (e.g., evolutionarily significant units) (Table 4).

Discussion

Integration of Evolutionary Concepts into Policy

The degree to which evolutionary concepts are discussed in conservation policy at different scales was highly variable. Our findings support concerns that international policy is failing to drive better incorporation of evolutionary concepts in conservation policy (Laikre et al. 2010).

The failures at the international level are largely mirrored in national-level policies. We found little discussion of the relevance of key evolutionary concepts in conservation policy in the three countries we evaluated. Given the emphasis on science and conservation in these countries, they could be viewed as best-case scenarios. Despite little direction from international or national conservation policies (Fig. 1a & 3a), there is provincial leadership in Australian policy, where the relevance of a wide range of evolutionary concepts is at least acknowledged (Fig. 3b). The reasons behind this leadership are unclear but may relate to the presence of evolutionary biologists in some management organizations driving a more evolutionary-focused agenda. This trend is unlikely to be the result of the scale at which policies are developed because it was not seen in Canadian and South African provinces (Fig. 3b).

There is wide recognition in international policies of the importance of maintaining GD when managing biodiversity, although this recognition was as low as 20% at the national level (Fig. 1). Despite overwhelming evidence from the peer-reviewed literature for the benefits to biodiversity of maintaining GD (Hoffmann & Sgrò 2011; Sgrò et al. 2011), the discussion of this issue in conservation policy is superficial. Conservation science appears to have been successful at raising awareness about the problem, especially as it relates to threatened species management (Fig. 2). However, this is not translating into a strong understanding of how to change management practices. Contributing to the perception that decision makers do not understand how to manage GD (e.g., Frankham 2010; Hoban et al. 2013) is the general failure of policies to make a direct connection to the reasons GD is important (e.g., contributing to the long-term resilience and adaptive potential of populations) (Fig. 1).

Although general evolutionary concepts are mentioned in conservation policy, we found little discussion of specific evolutionary concepts linked to GD (Table 1). Outbreeding depression and mating systems were rarely mentioned in any policies (Fig. 3). There was slightly higher recognition of the importance of life-history strategies, inbreeding depression, and gene flow to conservation (Fig. 3b), although not approaching the level of emphasis given to life-history strategies and gene flow in the conservation literature (Fig. 3c). Although Australian provincial policies were far more advanced than other jurisdictions (Fig. 3), there was little discussion of the practical application of these concepts. To address this low level of recognition of the importance of evolutionary biology, it will be important to identify the barriers to better integrate these concepts. In particular, there is a need to determine what would help practitioners change their practices and to provide more training in evolutionary biology for practitioners.

Table 4. Suggested policy areas where the scientific community does not agree.*

<i>Concept</i>	<i>Type of guidance</i>	<i>Contrary evidence</i>	<i>Recommended action and research</i>
Monitor genetic diversity	Use next-generation technology to monitor genetic diversity (20,29). Monitoring over time will provide insight into population processes (30).	Molecular diversity in neutral markers is only weakly correlated with adaptive potential, so what matters is not being monitored (31, 29).	Focus on genome-wide measures of diversity to provide insight into both adaptive and neutral processes (29).
Connectivity	Reconnect populations to allow for gene flow that can maintain genetic diversity (14).	High gene flow can inhibit local adaptation and the evolutionary response of populations (32). Connectivity can facilitate invasion (20).	Genomic data can provide more comprehensive assessment of gene flow and the relative risks of gene flow to local adaptation. (29). Ensure decisions around connectivity are considered within a risk-assessment framework (e.g., 14, 29).
Gene flow	Gene flow prevents inbreeding and the effects of genetic drift. This can be achieved through one migrant per generation (33).	There needs to be movement of several individuals per generation (14).	Genomic data can provide more comprehensive assessments of the benefits of gene flow (29). More research should be targeted at the level of gene flow required to prevent inbreeding. Use risk assessments (e.g., 14, 29) to guide decisions around connectivity.
Hybridization	Hybridization threatens population persistence and can lead to extinction (34).	Hybridization can prevent species extinction and lead to adaptive evolution that facilitates ecological shifts (35) (see Table 3 genetic rescue).	Genomic evidence suggests hybridization need not abolish local adaptation and that genomic extinction through hybridization is unlikely to occur (29). Combine genomic data with assessment of fertility of F1 hybrids (where possible) to monitor effects of hybridization.
Species concept	Species show reproductive isolation, independent evolutionary fates, and populations can exchange genes without adverse effects (36).	Species show distinct differences in genetic markers that can be used to determine distinct groups (37).	Use the increased power and resolution of genomic data to resolve taxonomic uncertainties (29).
Evolutionarily significant units (method to identify populations that are distinct and should not be interbred; no agreed definition)	Generally defined by neutral genetic diversity, length of isolation (38), and ecological differences (39). Avoid mixing to preserve genetic distinctness, maintain local adaptation, and avoid outbreeding depression.	Should be defined based on adaptive significance not neutral diversity (40). Greater mixing is favored to maintain genetic diversity and adaptive potential (14). There are new approaches to assess the risk of outbreeding depression (1).	The risk of outbreeding depression has been overstated (2, 14) and the benefits of mixing populations, especially when small and inbred, are clear (1, 41). Use risk assessments (2, 6, 14), combined with genomic data when possible (29) to guide decisions about when to mix isolated populations.

*Numbers in parentheses refer to references provided in Supporting Information.

Link between Policy and Applied Evolution Science

The divide between science and policy is often attributed to practitioners' inability to access and understand the relevant science (Fuller et al. 2014). Yet there has been little critical evaluation of the degree to which the conservation literature provides practitioners with the necessary evidence to support their decisions (but see Fazey et al. 2005). Practitioners need an evidence base with which to evaluate the risks and benefits of changing existing policies and practices (Frankham 2010; Hoban et al. 2013). In general, conservation policy is lagging behind

the literature in integrating evolutionary concepts (Figs. 1 & 3). However, we found that the science is not always in place to allow practitioners to judge the risks and benefits of changing management practices, and in some cases disagreement within the scientific community could lead to confusion among practitioners (Table 4). Despite strong advocacy for the need to change conservation practices (e.g., Frankham 2010; Weeks et al. 2011), many authors have highlighted the need for more tools to support conservation practitioners make the necessary changes (e.g., Frankham 2010; Carroll et al. 2014). In several

cases, general recommendations were not accompanied by the specific guidance practitioners need to interpret broad recommendations for their management context (Table 3).

Evolutionary concepts have had little penetration in management of invasive species (Fig. 2). There is evidence from agricultural studies (greenhouse and field trials) that management practices can help avoid the evolution of herbicide and pesticide resistance (e.g., Tabashnik et al. 2013; Neve et al. 2014). Despite calls for similar management strategies in conservation (Smith et al. 2014), we know of no studies that test this approach in a conservation context or provide clear guidance about when herbicide resistance is likely to become a problem for a target species. Differences between the objectives of agriculture and conservation may prevent direct translation of management strategies.

Within the literature, the lack of agreed-upon definitions for relevant concepts may contribute to poor integration of evolution in conservation policy. For example, confusion around the definition of evolutionarily significant units (e.g., Table 4), a potential tool to guide decisions about when populations should remain separated (Frankham 2010), could be contributing to risk aversion associated with gene-pool mixing to restore GD (e.g., genetic rescue) (Weeks et al. 2011). Adding to the confusion is the lack of a clear definition of what constitutes a discrete species (Frankham 2010). These controversies and the complexity of the risks associated with changing management practices (e.g., Byrne et al. 2011) may be contributing to the low uptake of evolutionary biology in conservation policy.

Although there are important gaps in the evidence base that conservation practitioners need to adapt their management practices, there are notable examples of rigorous decision-support tools (Table 3). Despite the strong relevance of several decision-support tools to the Australian management context (e.g., Broadhurst et al. 2008; Byrne et al. 2011), we found no mention of them in Australian conservation policies. Even within policies specific to threatened species or managing fragmented landscapes there was little discussion of the risks and benefits of gene flow. The omission of existing decision-support tools from policies suggest these factors may be only superficially considered when making management decisions. However, the operational context may also be a barrier to implementing some recommendations from the literature, such as maintaining large connected populations in landscapes where multiple threats operate.

The existing decision-support tools for integrating evolutionary concepts into management (Table 3) consistently highlight the many interacting factors (5–12) relevant to the risks of potential management actions (Byrne et al. 2011; Frankham et al. 2011). Similarly, some management solutions may have both negative and positive

outcomes. For example, restoring connectivity to improve GD for native species also facilitates the spread of pests and diseases (Carroll 2011). Given this complexity, designing risk-assessment tools requires a large evidence base across many management contexts and over long time frames (Frankham 2010; Byrne et al. 2011). The conservation-focused evidence base is primarily of low quality because it relies largely on model organisms, laboratory, and greenhouse experiments (e.g., 69%; Frankham 2015), or studies from disciplines with different management contexts (e.g., agricultural). Although these studies provide good general guidance (Smith et al. 2014), there is also a need for more applied evolutionary research to help guide effective policy development (Hoban et al. 2013).

Conservation practitioners have limited resources and competing management priorities, potentially making them reluctant to change management strategies without clear evidence for better outcomes (Cook et al. 2016). The absence of specific guidance for practical action and of evidence of the effectiveness of alternative management actions may be important barriers to greater integration of evolutionary biology (Carroll et al. 2014). These shortfalls provide opportunities for evolutionary biologists to direct their research toward informing policy. However, our results suggest barriers to greater integration of evolutionary concepts are more complex than the availability of decision-support tools. Other potential barriers include practitioners having a limited understanding of evolution (Ashley et al. 2003; Frankham 2010). There is a clear need to increase the representation of evolutionary biologists within conservation biology and to help them engage with practitioners. They can help practitioners understand relevant evolutionary concepts and determine how to integrate evolutionary concepts in management decisions. Better engagement by evolutionary biologists could include participating in advisory committees and threatened species recovery teams and developing decision-support tools in collaboration with practitioners (Cook et al. 2013). Embedding evolutionary biologists in management agencies and ensuring evolutionary biology is taught in conservation-relevant training programs could also increase the knowledge and capacity of practitioners (Cook et al. 2013). Without this engagement by the evolutionary biology community, evolutionarily enlightened management is unlikely.

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Supporting Information

A list of legislation and policy documents used in the content analysis (Appendix S1); number of relevant policy documents in the content analysis at the provincial scale (Appendix S2); frequency with which evolutionary concepts relevant to conservation are mentioned in provincial policy documents in Australia (Appendix S3), Canada (Appendix S4), and South Africa (Appendix S5); and supplementary references for Tables 3 and 4 (Appendix S6) are available online. The authors are solely responsible for the content and functionality of these materials. Queries (other than absence of the material) should be directed to the corresponding author.

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