

KEY ELEMENTS OF BIODIVERSITY IN BRITISH COLUMBIA: SOME EXAMPLES FROM THE TERRESTRIAL AND FRESHWATER AQUATIC REALM

Prepared for Conservation Planning Tools Committee¹

MAY, 2007

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ACKNOWLEDGEMENTS

The following people provided helpful input into this project: Rob Cannings (RBCM), Elizabeth Elle (SFU), Martin Carver (MoE), Ted Down (MoE), Deb Mackillop (MoF), Bruce Marcot (USFS), Steve McAdam (MoE), Diane Scrivastava (UBC), Jordan Rosenfeld (MoE) and Greg Utzig (Kutenai Nature Investigations Ltd).

Tory Stevens (MoE) provided much feedback, context and review. Internal review of an earlier draft was provided by: Matt Austin (MoE), Jan Kirkby (Environment Canada), Marian Adair (Nature Trust), Geoff Scudder (Nature Trust), Dan Buffet (Ducks Unlimited) and Andy Mackinnon (ILMB).

We thank everyone for their input.

TABLE OF CONTENTS

EXECUTIVE SUMMARY	IV
SECTION 1. A FRAMEWORK FOR IDENTIFYING KEY ELEMENTS	1
1.1. Objective and Scope.....	1
1.2. Review of Concepts.....	1
1.3. Functional Species: a brief review	2
1.4. A Framework for identifying key elements	5
1.5. Key Ecosystems and Processes.....	7
1.6. Potential Key Elements for BC	8
1.7. Additional Key Elements already under Management Focus in BC	13
SECTION 2. RESULTS – EXAMPLE KEY ELEMENTS.....	14
2.1. Key Terrestrial Species: Gray Wolf (<i>Canis lupus</i>)	14
2.2. Key Terrestrial Species: North American Beaver.....	17
2.3. Key Terrestrial Species: Red-backed voles.....	20
2.4. Key Terrestrial Habitats: Cottonwood Ecosystems	22
2.5. Key Terrestrial Habitat/ ecosystem: Wetlands in Dry Ecosystems.....	25
2.6. Key Terrestrial Habitat: Broadleaf Trees.....	28
2.7. Key Terrestrial Process: Cyanolichens and Nitrogen Fixation.....	30
2.8. Key Terrestrial Process: Faunal Pedoturbation	33
2.9. Key Terrestrial Process: Insect Pollination.....	36
2.10. Key Freshwater Species: Anadromous Salmonids	38
2.11. Key Freshwater Species: Kokanee	41
2.12. Key Freshwater Habitat: River Floodplains	44
2.13. Key Freshwater Habitat: Lake – Tributary Confluences.....	47
2.14. Key Freshwater Habitat: Estuaries.....	49
2.15. Key Freshwater Process: River Flow Regime.....	52
2.16. Key Freshwater Process: Lake Levels.....	56
2.17. Key Freshwater Process: Groundwater-Surface Water Interactions	59
FRAMEWORK REFERENCES.....	64
APPENDIX 1: SUMMARY OF THE NUMBER OF KEY ECOLOGICAL FUNCTIONS PLAYED BY VERTEBRATE SPECIES IN THE COLUMBIA BASIN.....	66

EXECUTIVE SUMMARY

WHAT ARE KEY ELEMENTS AND CAN THEY BE IDENTIFIED?

The Biodiversity Action Plan is identifying a range of different aspects of biodiversity that require focused management in order to maintain the biodiversity values in British Columbia. This background report was commissioned to explore the concept of biodiversity 'key elements' – those elements that are particularly important from a functional perspective. Where possible, the objective was to identify some key elements of biodiversity in BC organised into three organisational scales – species, habitats and processes.

Typically, functional importance has been described at the level of species. And the functional importance of 'keystone' species has long been recognised: these are species that have a greater functional importance than suggested by their biomass. Alternatively, 'foundation' species are also known to be functionally important, precisely because of their commonness within an ecosystem. However, as the relative distribution and abundance of species changes with landuse change the distinction between keystone and foundation species becomes difficult to differentiate. As formerly common foundation species become rarer they can effectively become 'keystone' species as their populations are reduced to low levels.

We are therefore defining a new term - key elements of biodiversity – which embraces the importance of species that have a high functional interaction with other elements, and are prioritised for action on the basis of their population status. Key elements include species that are either naturally relatively rare (as in keystone species) or are becoming rare (as in foundation species). Either way, current or future loss of key species is predicted to have a disproportionate influence on biodiversity.

Considering functional importance is the converse of asking whether a particular species or element is functionally redundant (sensu Walker 1992). It has been proposed that species or elements may be 'redundant' if they are weakly interactive with other species, or if there are a number of other elements which play an exact or similar role. It is worth noting that the concept of redundancy has been heavily criticised for being difficult to determine with any certainty (e.g. Rosenfeld 2001).

Applying these concepts that are derived for single species to other scales of biodiversity, such as habitats and processes, is difficult. However, there is utility in attempting this exercise since presumably the loss of particular habitats or processes can have different levels of functional influence. Although it is intuitively unlikely that the concept of redundancy can be applied to either habitat or processes, presumably there is a relative scale of functional importance even within these important elements of biodiversity.

Conservation scientists have discussed the question of functional importance and suggested that functionally important species and elements should be the focus of conservation management. However, in this review we have found no example where function has been thoroughly integrated into a management planning process. Although noted as a good place to focus management attention, examples fall back on the notion that there is insufficient science to properly identify these key elements (Soule et al. 2003). In this work, we come to a similar conclusion – academics and managers express interest in the concept, but there is little systematic science sufficient to identify a short-list of the most important functional elements in BC.

Factors which make identification difficult include:

- functional importance occurs at multiple scales – for instance dragonflies may be the functionally central predator within an ephemeral pond, and wolves may play the same role in northern ecosystems. Each is equally “important” in its ecosystem, and the functioning of each ecosystem may be radically altered if the predator is removed. Wolves clearly have a larger physical footprint, but a large number of listed species may inhabit the grassland pond that is maintained by the dragonflies;
- functional importance will vary in different habitats or ecosystems. It may be necessary then to attempt to develop a list of the key elements occurring across a suite of different habitat types in BC.
- functional importance may differ seasonally, or with the particular context of an ecosystem type⁴.
- basic functional importance is likely dominated by fundamental processes, the details of which and how they interact with the species and habitats within which they play a part are largely unknown. An example is nitrogen cycling since most forested ecosystems in BC are nitrogen limited, and so the processes that make nitrogen available are fundamental to the overall functioning of the ecosystem.

EXAMPLE KEY ELEMENTS FOR BC

Within the constraints of available science, we provide a framework for identifying key elements, and use it to explore the identification of potential key elements of biodiversity for BC, in the terrestrial and in the aquatic realm. The framework includes two questions: a) whether the element has strong functional importance (or interaction) and b) whether the element is relatively rare (a keystone) or potentially becoming rare locally or provincially (a foundation species under threat) that sufficient loss to impact function is possible.

The first half of the definition really asks about how an element interacts with its surroundings, and whether theoretically it fundamentally influences biodiversity values through function. The second half of the definition speaks to whether the element is sufficiently vulnerable that we should be concerned about the potential loss of its functions.

Additionally, in order to prioritise elements for inclusion in this report, MoE determined that this work should focus on key elements of BC's biodiversity that *currently are not the focus of management*. Many of the more obvious functionally important elements of biodiversity in BC are already under some form of management and these examples are not further explored here.⁵ Examples of elements we do not discuss in this paper include:

- Species: individual salmon stocks (i.e. genetic variability), primary cavity nesters;
- Habitats: old growth forests, ungulate winter range; wildlife trees, coarse woody debris, endemic / listed species' hotspots;
- Processes: fire, climate change.

The key elements which are discussed were chosen because they were relatively widely applicable in BC, because there was some scientific evidence the elements are key, or because they illustrated a point about the complexities of determining the functional importance of individual elements. We believe that the majority of elements identified here are high ranking key elements of biodiversity in BC⁶, and managing for them will improve the chances that

⁴ For example the typical keystone species *pisaster* only acts in this role on exposed shorelines and not on unexposed shorelines.

⁵ Note that it was not in the ToR to explore the adequacy of current management to maintain potential functions of these elements.

⁶ With the exception of red-backed voles, which are provided more as an example of potential importance at smaller scales.

conservation planning is effective. However, we don't believe there is a way to systematically determine THE key elements of biodiversity, since the specific relevant element will vary by ecosystem, by spatial scale, and likely through time or context in a particular ecosystem.

APPLYING THE KEY ELEMENTS CONCEPT WITHIN CONSERVATION PLANNING

This project has examined the feasibility of using a 'key element' concept as one piece of a conservation planning framework for BC. Although it was outside the terms of reference of the project, a discussion of how the concept can be used, in relation to other approaches to conservation planning is needed, and is provided in the broader Biodiversity Action Plan.

It was suggested by a reviewer that the concept of key elements seemed infeasible within a conservation planning framework because the ideas or examples are complex, non-representative and difficult to monitor. We would agree that this is the case, and is very likely why the concept has generally not been applied.

A number of conclusions arise from investigating these ideas:

- Functional importance is a central concept within ecology, and should be embraced at all levels of conservation planning; i.e., the test for successful conservation planning should be to ask whether the element being managed is at sufficient levels to maintain its functional roles;
- Functional importance is already an integral part of the conservation planning process in BC, though perhaps only intuitively. Many of the elements already chosen for management (e.g. coarse filter, ungulate winter range, genetically variable fish stocks, fire management) are key functional elements;
- Some of the suggestions for 'key elements' from the CPTC (e.g. global importance, endemic species, listed-species, biodiversity hotspots) do not necessarily fit the criteria of having strong interactions / high functional importance. This is of course not to say that they should not be a central part of a Biodiversity Action Plan, but it is outside the scope of this project to assess the utility of different approaches to planning.
- Invasive species are clearly functionally important for biodiversity in BC. The Biodiversity Action Plan will deal separately with invasive species however (T. Stevens pers. comm.).

Overall we suggest the concept of key functional elements may have limited immediate utility since it is difficult to apply. However, the concepts are likely be an important component of a successful conservation strategy and should be retained within the framework and used where information exists, or as new information is developed.

Section 1. A FRAMEWORK FOR IDENTIFYING KEY ELEMENTS

1.1. OBJECTIVE AND SCOPE

This work was commissioned as a background status report for the development of a Biodiversity Action Plan for the province of British Columbia. Attempting to directly manage for and maintain all aspects of biodiversity is both conceptually and logistically difficult, and many approaches to simplifying this task have been suggested. This document provides background and examples for one such approach – the identification and management of key elements of biodiversity⁷.

The document provides an overview of how key elements might be defined and identified. We then provide examples at multiple scales of how the concept may be usefully applied within the terrestrial and freshwater aquatic realms. A number of examples of potential key elements are then discussed. The contract asked us to identify about nine key elements of biodiversity in each realm, with 3 at each scale of species, habitat and process.

In addition, a goal of the project was not simply to identify key elements of biodiversity but also to consider areas that were being missed by current management approaches and could be the central part of the Biodiversity Action Plan. This second element put a quite different focus on the project and as a result some of the more obvious key elements of biodiversity in BC were not highlighted here because they are already the focus of specific management efforts (see Section 1.7).

Although much discussed, the concept of functionality has rarely been used in conservation planning and is only recently becoming a central theme within research. We believe that the majority of elements identified here are high ranking key elements of biodiversity in BC⁸. However, we don't believe there is a way to systematically determine THE key elements of biodiversity, since the specific relevant element will vary by ecosystem, by spatial scale, and likely through time or context in a particular ecosystem. In order to apply the key element approach more systematically throughout BC, we suggest that each individual ecosystem should be considered in isolation to assess ecosystem-specific key elements.

1.2. REVIEW OF CONCEPTS⁹

Attempts to manage or maintain 'biodiversity' have often fallen back on the use of 'surrogates,' or 'indicators' (Franklin 1993; Caro and O'Doherty 1998). Indicators can be defined as organisms or physical or ecological parameters whose characteristics are used as an index of attributes too difficult, inconvenient or expensive to measure directly (Landres et al. 1988). Different aspects of biodiversity require different types of indicators:

Indicators for environmental conditions:

- environmental health indicators (e.g. species or guilds of species sensitive to particular toxins or disturbances)

Indicators for biodiversity parameters:

⁷ A wide range of other reports are developed and will be placed into a systematic framework within the Biodiversity Action Plan. It is not part of the terms of reference for this project to place key elements in the broader context.

⁸ With the exception of red-backed voles, which are provided more as an example of potential importance at smaller scales.

⁹ In this overview, we focus on species primarily, but also apply the ideas of key elements to ecosystems and ecological processes.

- 'indicators of high biodiversity' provide information about locations of high abundance or diversity;
- 'umbrella species' provide information on likely trends of multiple alternate species;
- flagship species are used to focus on a geographic area or issue by creating social and political pressure.

None of these consider how each indicator interacts with its environment. An alternative approach is to use functional indicators:

- keystone species are defined as species that have a disproportionate influence on biodiversity, more than might be suggested by their abundance or biomass;
- foundation species have an important functional role in the ecosystem but it is not necessarily disproportionate to abundance or biomass, because they are usually abundant.

Both keystone and foundation species can be classified as 'strong interactors' (Soule et al. 2003) and their removal from an ecosystem will result in significant ecosystem change because of their functional interactions with other biodiversity elements. Note that neither have typically been the focus of conservation efforts because of the lack of scientific understanding of interactions, and difficulties in identifying particularly strong interacting species. These two types of indicators are the focus of the remainder of this paper.

1.3. FUNCTIONAL SPECIES: A BRIEF REVIEW

The concept that some species have high functional importance in an ecosystem is well known.

Keystone Species:

A keystone species has historically been described as a species that has a disproportionate effect on its environment relative to its abundance. The analogy with the 'keystone' in an arch is used because although the keystone doesn't appear to bear any extra weight the arch will collapse without it. Similarly, if a keystone species is removed an ecosystem may experience a dramatic (and likely unexpected) shift, even though that species was a small part of the ecosystem by measures of biomass, abundance or productivity (Paine 1995).

Paine's example was that of the starfish predator '*Pisaster*'. Removal of starfish caused a series of unpredicted events within the intertidal community, including a huge increase in the density of one of its prey species (mussels), which through interspecific competition dramatically reduced the diversity of the shellfish community (Paine 1966, 1969). The keystone concept has been very popular in scientific literature since then, particularly within the growing science of conservation (Bond 1993; Bond 2001; deMaynadier and Hunter 1994; Hurlbert 1997; Khanina 1998; Mills et al. 1993; Piraino and Fanelli 1999; Power and Mills 1995; Vanclay 1999).

The idea that the loss of a single species may have large consequences that 'cascade' throughout communities is clearly relevant in a conservation context. Although conceptually pleasing, there has been intense debate about the utility of the keystone species concept, with concerns raised including:

- the inability to detect keystone species experimentally, except in limited cases. This is relevant to practical conservation measures because if likely species can't be easily detected then the tool cannot be applied;
- determining whether the test of 'disproportionate impact' is met, i.e. is it possible to define and differentiate between a keystone and other 'important' species such as

foundation species. This has raised intense academic debate but as outlined below we don't believe this issue is necessarily relevant in a conservation context;

- issues around the idea that only predators really fit the original definitions laid out by Paine;
- whether it is possible to identify which species actually is the keystone. For example, sea otters have been considered a typical example of a keystone predator. Their foraging actions result in maintenance of kelp forests and associated communities. However, changes in behaviour of Orcas has been more recently recognised to limit the sea otter population, causing a similar cascade through the ecosystem but with Orcas as the 'key'.

A number of authors have tried to provide answers to these questions to allow the concept to be developed, including providing:

- definitions of 'community interaction' which attempt to quantify how disproportionate the effect needs to be (Power et al. 1996);
- examples of approaches to identification of keystone species without removal from ecosystems (e.g. Davic 2000; Davic 2003).

Foundation Species:

'Foundation' (sometimes referred to as dominant) species are those that have high functional importance as a result of their commonness in the ecosystem. Removal of these species will, like keystone species, have a large effect on surrounding biodiversity simply because they are common, however until recently they have received relatively little conservation focus simply because of their perceived commonness. Examples include elements such as common predators, wildlife trees, dominant tree species within forested ecosystems, kelp in kelp forests, coral on coral reefs.

Combining the concepts:

The essential difference between the concepts of keystone and foundation species is biomass or commonness within an ecosystem. However, practically differentiating between these two has been shown to be theoretically difficult, and is further complicated as many formerly common species become rare and as changes occur so rapidly in many areas that the future of many species is unpredictable. Following this point we therefore identify a new term: key species - those with a high functional importance plus the potential for significant loss. This includes true 'keystone' species which are naturally rare, and foundation species which have the potential to be significantly impacted by current land use practices. This idea is supported by others (e.g. Soule and Noss 1998) who suggest that conservation efforts should focus on the broader issue of identifying **'highly interactive' species, irrespective of their biomass.**

IDENTIFYING KEY SPECIES¹⁰

Key functional species have been identified which have different types of functional roles within a community, including:

Organisms controlling potential dominants: here competition between multiple species is reduced by a species at a higher trophic level.

- the typical example is a predator such as the starfish *Pisaster*;

¹⁰ We know of no similar descriptions applying different concepts to habitats and processes.

- dominant herbivores may suppress potentially dominant plant species, and thereby maintain a more diverse community of less competitive species (e.g. loss of elephants from the savannah can result in a significant change from a grass-dominated community to a forested community, with the many resulting cascading changes in communities and species diversity¹¹;
- very small herbivores also can have such effects. For example slugs and snails removed a very small amount of vegetation, but created a change in community structure by changing seedling recruitment patterns in a grassland (Hanley et al. 1995);
- Diseases may also fit under this heading, such as anthrax or species-specific pathogens such as Dutch Elm disease which decimated elm tree populations and presumably had large impacts on their associated communities.

Resource Providers: these may be key to an ecosystem functioning if they provide a vital resource to a community at a time of scarcity. Most examples come from the tropics, but may be relevant here.

- many plants, for example, a seasonal fruit supply that provides resources at a critical time;
- salmon might be considered within this realm, since they have such wide-ranging community impacts;
- fig genus which has many closely associated species is a well cited example;
- possible examples are nutrient providers (e.g. an example suggested of a symbiotic nutrient fixer that provides resources to a nutrient-limited forest community).

Mutualists: where species' life-histories are intimately linked removal of one will likely result in significant changes to the other. The relevance of this category may increase considering 'group' mutualists (e.g. pollinators and a group of specific plants).

- mycorrhizae;
- orchids have been shown to have co-evolved with specific specialist pollinators;
- the keystone definition may apply more appropriately where a number of species are reliant on a single mutualist, for example a guild of 8 plant species all dependent on a single species of fly for pollination;
- even a two-species mutualism might be key if one of the species has a strong interaction with other species (e.g. a pollinator of a dominant plant species; e.g. fig wasp impacting fig trees which has significant impacts on the surrounding forest community).

Ecosystem Engineers: some species cause significant structural changes in the community, resulting in significant effects on other community members (term coined by Jones et al. 1994).

- many trees;
- the beaver is a typical example of this type of keystone, affecting both the terrestrial and aquatic environment (Naimen et al. 1988);

¹¹ Large herbivores may not fit the definition of keystone because of their large biomass, however small herbivores have been shown to have a similar effect, e.g. kangaroo rats in the Chihuahuan desert whose removal caused huge impacts (Brown and Heske 1990).

- grazers that keep vegetation in an early seral stage, which is more productive than a late seral stage;
- Various burrowing animals result in significant soil disturbance and cascading impacts;
- Ants and termite nests;
- Hole drilling by woodpeckers and sapsuckers which provide both food and shelter to a wide range of other species.

EXCLUSIVITY OF A FUNCTIONAL ROLE

In any of the above categories, the functional importance of a particular species will vary depending how many other species also function in that particular role. If, for example, a large community of ungulate species maintain a particular grassland ecosystem in a particular state, then removal of an individual species from that community may have little functional importance. If though, a single species is primarily responsible for the grazing pressure, and no others are likely to move into that role after its removal, then the functional importance of removing it will be much more visible.

The difficulty in applying this concept is that we know that many species are quite plastic in their behaviour, and removal of a single species may result in other species 'moving' to fill a particular niche or function. Available science on the plasticity of functions in response to changes in community structure is very limited.

In two of the categories – mutualists and resource providers – the importance of these roles is particularly tied to the exclusivity of the relationship between species. There seem to be a reasonable number of examples of highly interactive species from the tropics (e.g. figs and figwasps; suites of pollinators that use only a single plant). However, there appear to be relatively few that occur in BC; known examples include the Steller's jay and Garry oak, and Clark's nutcracker and white bark pine. There are also exclusive mutualists within the lichens and mycorrhizae groups. However, the relative paucity is perhaps unsurprising since the geologic context of BC has resulted in a very short time for co-evolution of life-history strategies. In general, we therefore expect that key species in BC are much more likely to be either 'species controlling other dominants' or 'ecosystem engineers', or resource providers that provide a general resource to a broad community rather than a specific limited resource to a single species.

1.4. A FRAMEWORK FOR IDENTIFYING KEY ELEMENTS

Our intent is to focus on key elements of biodiversity that have large and potentially cascading impacts on community structure and function, irrespective of their availability/ abundance in the ecosystem. We propose that a useful definition in a conservation context includes both:

- a) Species that have strong community influence, or have strong or multiple interactions with other species. The loss of such species would be expected to affect others in a cascading fashion. Species with very weak interactions or 'influence' in a community fit the idea of a 'redundant' species (Walker 1992), as removal of these species is predicted to have little effect on the functioning of the community¹². In addition, the influence of the species as it is removed will increase if the species is not readily replaced by another

¹² Note that there is significant debate as to the usefulness of the concept of redundancy when understanding of functional roles is relatively weak.

similarly functioning species. Although a useful idea, identifying such species is very difficult with any rigour, since species' interactions are very complex.

- b) Species that are either naturally rare or under pressures that result in decreases (or increases) in population sizes, as a result of human actions or natural changes. This is relevant because without meeting this test there is no urgency to address a particular species, even if it is a true keystone. For example, mule deer are an important foundation component of the food chain across BC. However, the likelihood of reducing the population to the point of observing cascading trophic impacts is very low because the species is not under threat of significant population decline. Similarly, the starfish *Pisaster* is a known example of a keystone species, but again, the population is not under threat so its priority would be lower. In summary: the relevance of 'threat' is related to whether we predict that the abundance of a species is in the process of being altered sufficiently to result in a significant change in function.

Together these two facets of the definition provide a way to prioritise potential key elements based on degree of functional importance and degree of threat. Figure 1 provides this framework in graphical format with four theoretical examples.

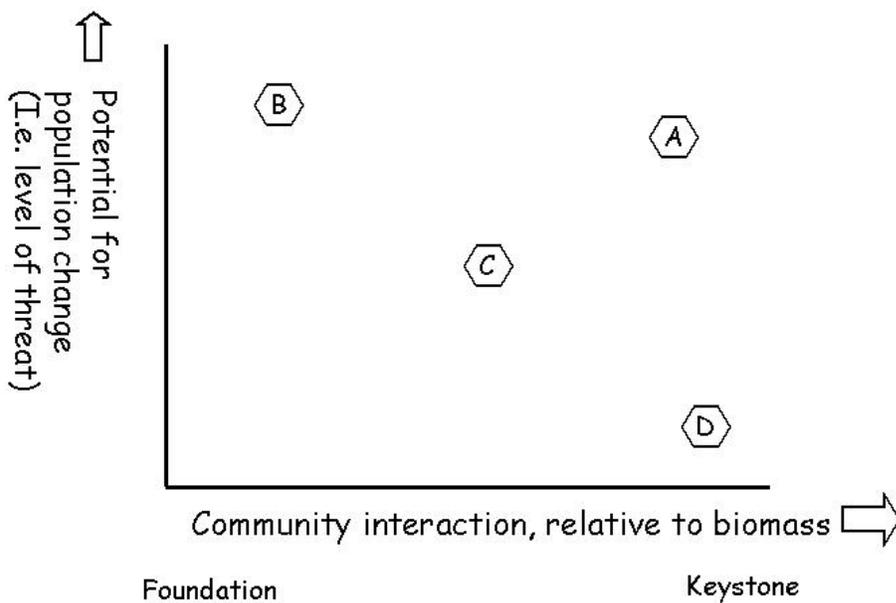


Figure 1. Level of functional interaction and probability of significant population change can together be used as a tool to prioritise key species that should be focused on in a conservation context. Species A and B would both be priorities. Species C may be a priority, but is of lower concern than either A or B. Species D is a true keystone, but is not a conservation priority because the population is stable.

OTHER FACTORS TO CONSIDER IN IDENTIFYING KEY ELEMENTS FOR BC

Key species may vary with a number of different factors:

- a) the ecosystem. There are many ecosystems in BC (within the groups of terrestrial and aquatic), so determining where to focus effort is difficult. Different ecosystems are highly likely to have different key elements (also see b);
- b) the community context of a species. Research has shown that in a foreshore community dominated by wave action, the 'quintessential keystone' *Pisaster* does not function as a keystone species as it does along less severe shorelines. Ecological context is therefore crucial. The types of factors that have been shown to influence 'keystone activity' include geographic space, gradients of productivity, physical factors and presence of other species;
- c) the position on the foodchain. Ecosystems can have numbers of co-dominant species, which occur at different levels on the foodchain. E.g. primary producers may be dominated by a particular grass, primary consumers by an herbivore, and secondary consumers by a predator. Each level may have its own key element.
- d) Real keystone species are still important because they have high community interactions, and are likely sensitive to population change because of their relatively low biomass. But their presence is likely difficult to predict without large-scale removal experiments. A review of traits of potential keystone species failed to find any common denominators (though it has been noted they are often predators with an ability to significantly impact their prey population, which in turn are often a significant predator / herbivore on another component of the ecosystem; Menge et al. 1994). Others have suggested approaches to identifying keystone species in advance, but have not been applied in a real context (Davic 2000). Trophic level may also be important because, for real keystones, having an important function that is proportionally higher than expected from biomass is easier if biomass is low (i.e. they tend to be higher up the foodchain)(Power et al. 1996). She notes here that inverted trophic pyramids are more common in aquatic ecosystems, so possibly herbivores or aquatic plant species are more likely to be keystones than their equivalents in terrestrial ecosystems.
- e) There is some level of evidence that where species' losses have already occurred, the remaining species may take on an increased keystone role, i.e. the functional importance of species may change as communities are simplified by species loss. i.e., as species redundancy is reduced. This ability to change functioning as ecosystems change will be highly relevant within the climate change scenario, but data are lacking on what might become key as climate changes.

1.5. KEY ECOSYSTEMS AND PROCESSES

The discussion to here has been primarily about identifying key element species since this has been the focus of literature on this subject. However, we were also asked in this project to apply the concepts to habitats / ecosystems and processes. Applying the concept of keystone to either ecosystems or processes has been criticised in the literature because it is not possible to apply the test of checking whether the influence is larger than that expected as a result of biomass (Payton et al. 2002). Considering 'functional importance' is only marginally easier. Additionally, identifying key ecosystems is perhaps also moot because by their nature, the loss of an 'ecosystem' will have significant cascading effects.

However, we suggest that the framework presented can be applied usefully in a general sense. Key ecosystems then would have higher functional importance than other ecosystems, and would be either naturally rare and therefore vulnerable, or typically common but under threat.

Useful factors for identifying potential 'key' habitats / ecosystems include:

- Those that interface with multiple other communities;
- Have high biodiversity (therefore may have higher cascading effects)
- Are relatively small or naturally uncommon and therefore vulnerable;
- Are vulnerable or under threat (irrespective of size).

Key processes are even more difficult to identify, because again any impact to processes will by definition have cascading influences through all or portions of an ecosystem. Possible criteria for identifying and ranking 'key' processes include:

- Processes which maintain ecosystems at multiple spatial and temporal scales (e.g. such as fire that profoundly impact the structure of whole ecosystems at multiple spatial and temporal scales);
- Processes where a 'mutualism' is involved, i.e. some community / species is specifically reliant on the process (e.g. nitrogen fixer and a nitrogen limited community).

As with species, we also consider whether there is a 'threat' to a particular ecosystem or process, in order to include it in our discussions. If there is no threat that the process / ecosystem, may be negatively impacted or lost in particular locations, then it becomes irrelevant to the conservation discussion, even if it has very high functional significance¹³.

1.6. POTENTIAL KEY ELEMENTS FOR BC

METHODS

In order to identify potential key elements of biodiversity for BC, we used a variety of approaches including:

- A review of the literature for suggestions of potential keystone, or key functional elements,
- A review of the Bio Gaps database (Holt et al. 2003),
- Interviews with a variety of experts in various fields in BC and the Pacific Northwest,
- Expert opinion of the authors,
- Examination of a 'key functional relationships' database (Marcot Undated), compiled for the Columbia Basin (Pandion 2001).

This last approach requires more explanation:

As highlighted in the introduction to this paper, species that have a large number of functions or have roles that they exclusively play will increase the probability that their removal from the ecosystem will have a significant effect. Developing Key Functional Databases has been advocated by Bruce Marcot, and a collaborative effort between the US and BC agencies has resulted in the Columbia Basin database.

¹³ Note that we're not sure we can state that anything has 'no threat' given the scenario of climate change.

This database attempts to identify all the functional interactions performed by individual vertebrate species for species in the Columbia Basin (Pandion 2001). We used it here to examine its utility in identifying individual species, or groups of species that play key ecological roles. The database can be used in a number of different ways:

- a) to identify species with the largest number of functions – these will presumably have a high or at least unpredictable impact if removed, and
- b) to identify species with unique functions or functions only carried out by a small number of species. The functions played by these species are unlikely to be replaced by others, so their functional interaction should be strong.

Using this database, I examined which species apparently had the most ecological functions. Table 1 is a summary of the top species (a full list is shown in Appendix 1). The range was from a high of 32 functions, to a low of 5. Using this simple rationale, each of these species could be ranked in terms of its potential interactiveness in the community. Clearly, the functional importance of each of these species differs according to the ecosystem being considered. Clearly deer mice and grizzly bears have very different landscape influence. However, this process also identifies why undertaking this process at different scales is such an important piece of the key element question.

It also is clear that the types of functions listed differ from each other in terms of their overall ecosystem effect, and that simply summing number of functions is not likely to be hugely useful in identifying overall key elements.

Table 1. Species with the highest number of 'functions' identified in the Key Ecological Functions database, for the Columbia Basin.

Species	Number of Functions
Black Bear	32
Raccoon	27
Deer Mouse	26
Beaver	24
Golden-mantled Ground Squirrel	24
Woodchuck	24
American Coot	23
Douglas' Squirrel	23
Red Squirrel	23
Grizzly Bear	22
Sandhill Crane	22
Striped Skunk	22
American Crow	21
Mallard	21
Black-billed Magpie	20
Common Raven	20

An alternative approach to using the database is to identify which types of functions are played by only a limited number of species. Figure 2 uses the broadest categories of 'function' to look at how numbers of species are distributed. It is reasonable to assume that removal of a species from the 'trophic relationships' group is likely to have less impact on trophic relationships in comparison with removal of a species from one of the smaller groups (e.g. soil relationships /

vegetation structure/ wood structure/ water relationships). In application, examining the more detailed set of functions (e.g. Figure 3) is likely to be more useful in identifying key functional elements.

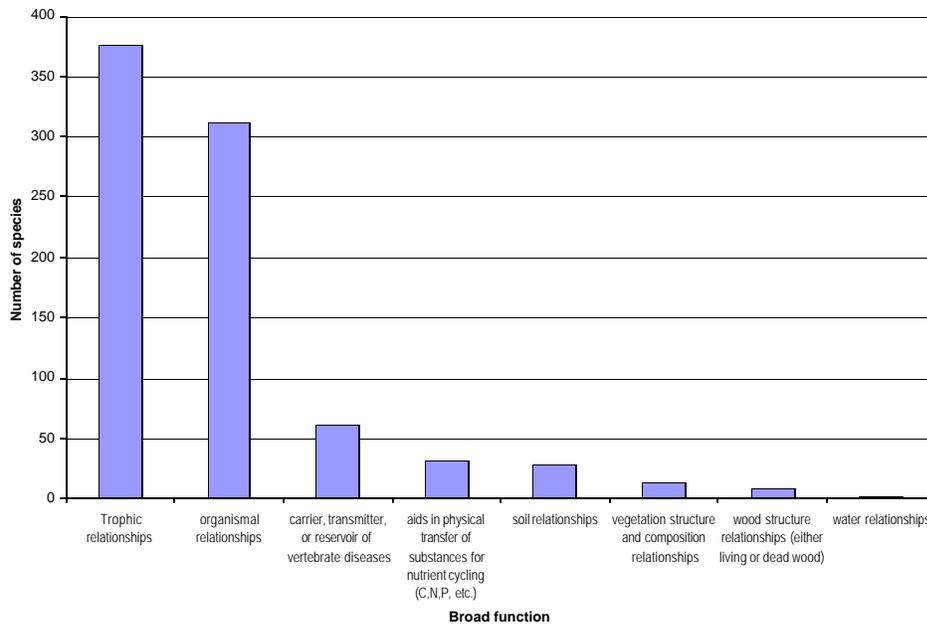


Figure 2. Number of species in each broad functional group.

At this more detailed level, species within the functional groups that perform that function on their own can be highlighted – e.g. functional group 1.1.2 (‘prey for secondary or tertiary consumer / primary or secondary predator = long-toed salamander), which only a single species is highlighted as performing. At this point our knowledge about the importance of different functions makes it difficult to determine whether in fact the long-toed salamander should therefore be identified as a key species on this basis. It may be reasonable to assume that this function has relatively little cascading influence throughout the broader ecosystem, however, we do not have the science to really determine this currently.

In contrast, the North American beaver is the only species identified as having the function of ‘impounding water’. This function is unique and is also known to have very wide-ranging influence across a range of both aquatic and terrestrial habitat types and communities. We are therefore on solid scientific ground in including the beaver as a key element because it is widely distributed across the province and affects large areas of both land and water.

Of the broad groups which have a relatively few species associated with them (see Figure 2), I examined each of the species in these groups and the twenty-nine species identified as having ‘soil relationships’ stood out because many of these species are already endangered. As a result, I focused a key process on this suite of species (see Biotic Pedoturbation) associated with an individual ecosystem.

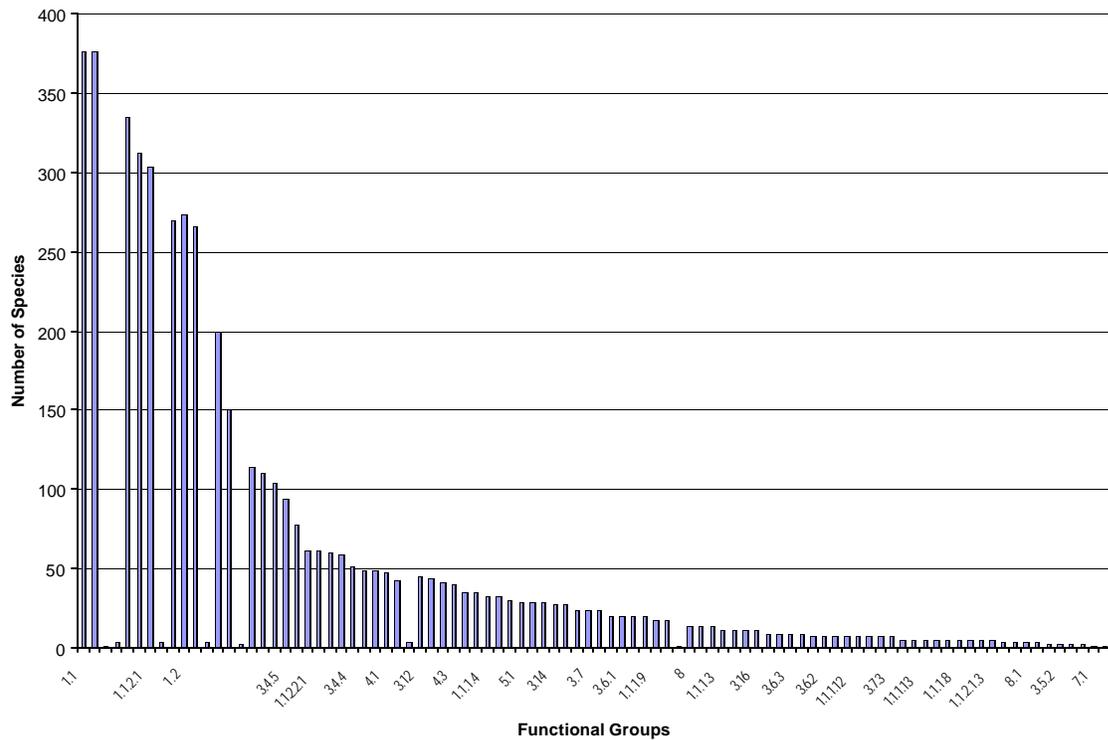


Figure 3. Number of species in each detailed functional group.

Using the key ecological functions database in this way was a useful exercise and provided useful output. Limitations of this approach include: the database is limited only to vertebrates, examination suggested some vertebrate species were missing from some categories, and the importance of each function to broader ecosystem functioning is not equal so it is difficult to use it to identify key functional elements.

EXAMPLE KEY ELEMENTS

As outlined in the Methods above, we used a number of approaches to identify potential key elements for biodiversity in BC. The initial goal for the project was to provide a ‘top 10’ list of elements, but we determined after reviewing the literature and other conservation plans that there was no systematic basis upon which to do this.

We therefore tried to provide a range of potential key elements that covered a variety of ecosystems, ideas, functions and scales. See Table 2 for a description of why each element was included here. Of the elements chosen as examples, we believe from the literature that each is a ‘key element’ for the functioning of BC biodiversity. However, we do not believe it is possible to identify *the most important set*, since we believe there are many additional factors to consider, including specific ecosystems, timeframe, scale etc.

Table 2. Summary and Rationale of Key Element Examples

Type	Example	Rationale for choice
Species	Gray Wolf	Suggested as a keystone species by literature, though more likely a 'strong interactor'. As a top predator demonstrated huge changes resulting from changing populations of wolves. Known to be increasing in some areas of BC, and decreasing in others. Although are part of management strategies is there a coherent management strategy that considers functional importance ?
Species	North American Beaver	One of very few examples of true keystone species. Highlighted by the key functions' database. Not at risk overall, but historic impacts on some populations due to damming of large and small river systems. Potential to be impacted by extensive small scale hydro schemes occurring throughout BC. Examine historic impacts and assess whether reduced populations have resulted in loss of key habitat types. Input into restoration planning and future management of populations in these key areas.
Species	Red-backed vole	A mid-trophic species suggested as a keystone in literature, has cascading functions up and down. Old-growth associated so has potential to be removed from large areas of the landscape, however, overall, little threat to the species. Included as an example of how key species can operate at multiple scales. (Is not included in 'key functions' database, but similar species deer mouse was given a very high functional ranking).
Ecosystem	Cottonwood ecosystems	Known to have high functional importance. Very high biodiversity values as a habitat type, plus a wide range of functions as an overall ecosystem. Under very high threat from historic and current development. Plus is potentially impacted by climate change. Much is located on private land.
Ecosystem	Dry ecosystem wetlands (e.g. Southern Okanagan)	Very high diversity in these local areas. Wide range of functions. Under very high threat from historic and current development. Plus is potentially impacted by climate change. Much is located on private land. Provides a multi-scale discussion about functions. For example, dragonflies may be a key species within the key element of wetlands.
Ecosystem	Broadleaf trees and mycorrhizal fungi.	Is highlighted by research as a strong-interactor. Relevant to almost all BC. This example is different from cottonwood ecosystems, because those are known as having high biodiversity values whereas broadleaf trees in general in concert with mycorrhizal fungi broadleaves over the landscape have broad productivity implications. These species are selected against at the landscape scale, under standard forest management practices.
Process	Cyanolichens and nitrogen fixation	Cyanolichens thought to be limited to old-growth forests (typically coastal temperate rainforest and inland temperate rainforest. Provide a very important function in making nitrogen available to the ecosystem (in these nitrogen-limited ecosystems). Suggested by research to be declining because they are often not present in a stand within the rotation period of forestry activities, and are maintained only by very high levels of partial cutting. Unknown overall effects on productivity but may be very important.
Process	Biotic Pedoturbation	"Soil relationships" in the key functions database were limited to a relatively low number of vertebrates. It was additionally noted that a relatively large number of these are identified as threatened or endangered. Although we don't know the relative contribution of these compared with invertebrates, this may be a key area of concern, particularly in ecosystems where soil mixing is a key part of maintaining productivity. These species are very vulnerable to general development.

Type	Example	Rationale for choice
Process	Pollination	Fundamentally important process to plant sexual reproduction. Inter-dependence between many species. In some areas of the world this inter-dependence is extensive. In BC, many species are less co-evolved, however it may be an issue in some biodiverse areas which have been heavily impacted (e.g. grasslands). Highly uncertain question. Implications of this key process or ecosystem service have both direct biodiversity and economic relevance.
Species	Anadromous salmonids	Anadromous salmon are a group of species with wide-ranging relevance. They have a substantial influence on both terrestrial and aquatic species' abundance and distribution at multiple spatial and temporal scales. Important influence on nutrient status in freshwater systems.
Species	Kokanee	Kokanee are a native non-anadromous species. They are important in many coastal and inland lakes, are sensitive to change and have a high degree of influence on abundance and distribution of many terrestrial and aquatic species.
Ecosystem	River floodplains	Many aquatic species in BC are adapted to the seasonal flood dynamics that occur on river floodplains and make extensive use of these habitats. Seasonal flood dynamics are believed to enhance biological productivity and maintain diversity in many river systems. Floodplains provide important nutrients and habitat for aquatic and terrestrial species.
Ecosystem	Lake – tributary confluences	Lake – tributary confluences provide high productivity habitats for a wide range of aquatic and terrestrial species and are high productivity hot spots within lakes.
Ecosystem	Estuaries	Estuaries have high intrinsic productivity and provide key refuge habitat for critical life stages of many fish and invertebrates. This productivity is heavily exploited by aquatic and terrestrial species.
Process	Flow regime in rivers	Flow regime has a direct effect on habitat availability in streams, habitat quality, and additional direct and indirect effects on physical and biological processes. Abundance and distribution of fish and other organism is directly related to many habitat variables associated with flow regime.
Process	Lake levels	Emergent and submerged aquatic macrophytes are the dominant structural component of littoral habitats. They provide food and shelter for a wide variety of invertebrates, fish and wildlife. Fluctuating water levels are considered the most important factor determining vegetation patterns on lake shores.
Process	Groundwater-Surface Water Interactions	In most areas of BC there is a strong interaction between surface flows and groundwater resources. Groundwater release to surface water forms most of the base flow for many streams through periods of no precipitation, or during winter when precipitation is locked up as snow or ice. This base flow is of extreme importance to organisms such as fish, as it is often changes in base flow that have direct effects on fish fauna. Nutrients released to surface waters from the hyporheic zone are known to influence surface water quality and productivity.

1.7. ADDITIONAL KEY ELEMENTS ALREADY UNDER MANAGEMENT FOCUS IN BC

As outlined in the framework section, we suggest that both coarse filter type foundation elements as well as the more typically used keystone elements are relevant to the concept of 'key elements'. Combining these ideas with the level of threat to those elements provides an approach to prioritising key elements for conservation planning.

However, additional direction was given from the contract manager that elements which are already the focus of management attention in BC should not be highlighted in this project. Taking that into account there are a number of broad key elements which we do not discuss, in particular:

- Species: salmon stocks (i.e. genetic variability), primary cavity nesters;

- Habitats: coarse filter habitats such as old growth forests, ungulate winter range; wildlife trees, coarse woody debris, endemic / listed species' hotspots;
- Processes: fire, climate change.

Each of these would likely meet the criteria of very high importance key elements, since they each are generally relevant to a wide diversity of ecosystems, have large cascading impacts and are all significantly changed from natural levels due to land management approaches.

In addition, we believe there are a number of 'key elements' in a broader description – especially relating to process that deserve a mention, in particular climate change which represents a key challenge in managing aquatic habitat and fauna. Scientific data clearly indicate that the climate is changing and animal and plant distributions are responding to these changes (Parmesan and Yohe 2003). There are strong indications of changes in physical parameters of BC freshwater bodies. River temperatures and streamflow patterns have changed in response to global climate change and this trend is expected to continue (Leith and Whitfield 1998; Morrison et al. 2002). Freezing and thawing patterns on BC lakes have changed throughout the province over the last few decades (BC Ministry of Environment 2006). Continued climate change is expected to have severe impacts on fish abundance and distribution in BC through effects on precipitation, streamflow, water temperatures, and range changes in native and non-native species (e.g., Welch et al. 1998; Fayram and Sibley 2000; Stefan et al. 2001). Given these general predictions, how society as a whole should focus its efforts to maintain healthy aquatic habitats in BC is a question deserving of significant attention.

Section 2. RESULTS – EXAMPLE KEY ELEMENTS

2.1. KEY TERRESTRIAL SPECIES: GRAY WOLF (*CANIS LUPUS*)

WHY IS THIS SPECIES IMPORTANT?

Functional role:

This species, as a top predator, has the potential to directly limit prey populations, and as a result, create a cascade of additional effects. Population status varies with the area of the province – some areas have declining natural populations whereas other areas have increasing populations due to changes in prey abundance and distribution. Both population increases and decreases are therefore of interest in terms of potential functional response:

- As a top predator, the species has the potential to regulate prey communities, and changes in wolf populations are known to result in cascading changes in both prey population densities, prey community diversity and cascading impacts through vegetation distribution and abundance (see below). Because the species tends to live socially (and so relatively large numbers can be present in specific location) combined with relatively high reproductive rates, they have the ability to increase rapidly in an area and so have a significant and rapid impact on the rest of the community.
- Evidence for a functional role of wolves is available from large-scale natural experiments, combined with specific experiments (such as plots / exclosures) where wolves have been removed (typically by hunting pressure rather than habitat loss) and / or reintroduced. A case study of these effects is available from the US in areas such as Yellowstone where wolves have been extirpated and then reintroduced. It is hypothesised there that the

removal of wolves from the landscape, which occurred somewhere around 1925, combined with lack of hunting for large ungulates within the National Park, resulted in significant landscape simplification. Effects include significant loss of habitats such as riparian ecosystems due to over-browsing, and the loss of aspen from the forest canopy (Ripple and Larsen 2000). Behavioural changes in foraging patterns by elk under varying predation pressure resulted in increased aspen regeneration and growth in high-use wolf areas. Similar effects were shown for cottonwood ecosystems: areas with high predation risk (measured by visibility and escape possibilities) showed a release of cottonwood regeneration over the short period of 5 years after wolf reintroduction (Ripple et al. 2003).

- Ecosystem engineers such as beaver were also negatively influenced from the loss of riparian habitats, resulting in extensive landscape alteration from their natural state. It is difficult to identify the exact linkages between wolves, hunting and also climate change and fire suppression but there appears to be good evidence that the loss of wolves is at least partly responsible for these changes (Singer et al. 2001).
- The potential cascading effects of changes in ungulate populations have also been considered. Indirect effects on nutrient cycling, net primary production and disturbance regimes have all been hypothesised (Hobbs 1996). Ungulates can result in changes in litter availability and quality, affecting nitrogen mineralisation, plus they can add significant nitrogen to the soils directly. These effects can also cascade through the ecosystem resulting in changes to the composition of plant community indirectly (rather than directly through grazing). Influences on fire regimes are possible by changes in fuel loading with reduced fire impacts in forested ecosystems and increased potential for crown fires in grassland ecosystems (Hobbs 1996).
- In a similar study, the combined loss of grizzly bears and wolves from Yellowstone are attributed as the cause of a cascade of impacts, including the increase in moose and other ungulates, significant alteration of riparian habitats caused by herbivory and coincident reduction of avid neotropical migrants in the impacted willow communities. Avian species richness and nesting density varied inversely with moose abundance, and two riparian specialists were not found in areas with particularly high moose densities. This study is shown as evidence of top-down control (i.e. wolf-control) in this ecosystem. These cascading effects are known in general to affect bird and other species diversity, since habitat structure is known to be one of the best determinants of diversity (Wiens 1989).

Functional exclusivity:

In communities where there is an intact predator/ prey community a number other large predators have the potential to influence prey species populations (e.g. grizzly bears, black bears, wolverines, cougar). The debate about the extent to which any of these species really regulates populations as a single species, or in concert with other species, or the extent to which compensatory mortality is active, remains. However, in many natural systems it does appear that wolves can limit ungulate populations, though often this is in concert with effects from other predators and difficult to distinguish the exact sources of mortality and compensatory mortality.

Status and potential for future change:

Across the broad continent of North America, wolves historically existed from the Arctic south to Mexico. Within 300 years of European colonisation they had been essentially extirpated across the entire United States and Mexico, with healthy self-sustaining populations remaining only in Canada.

Within BC, wolf population status varies with different areas of the province. Wolves have been extirpated or are declining in many southern regions with higher human population densities. Relatively stable populations exist in many more northern regions where land use changes are relatively minor (e.g. the populations within the north eastern Muskwa-Kechika). Other areas are experiencing local increases as formerly continuous forest cover is replaced by younger stands, which results in an associated increase of prey species and appears to allow expansion of wolves' local ranges.

Overall, Gray wolves are generally not considered a species of conservation concern in BC (they are yellow-listed). However, their extensive extirpation from the vast majority of their historic range in North America, should be a red-flag for management and development in BC. Wolf populations in BC are in flux, and are under the influence of a range of different pressures, including land use changes creating habitat for prey species in formerly unsuitable habitat, hunting to manage prey densities at human-value determined levels, and the combined effects of hunting and poaching.

Relevance to BC:

Historically the gray wolf had one of the broadest ranges world-wide of any mammal and was distributed across North America and most of Eurasia. In BC, gray wolves are distributed throughout all the forested regions of BC. AN estimated total population size is given at 7500 animals (MoE 1998). Local population trends vary in different parts of the province. The effects of this species are broadly applicable throughout the ecosystems of BC, with gaps in their range only the very south and south west of the province.

CONSEQUENCE OF CHANGE OR LOSS

This species is proposed as a key element because of its potential functional importance in many ecosystems across BC. Local increases (such as in southern BC), following primary prey population increases have the potential to cause extirpation of red-listed mountain caribou herds (e.g. Bergerud 1998). Alternatively, local decreases in other areas (e.g. on the coast or in northern BC) have the potential to radically alter prey densities and ultimately result in landscape simplification as a result of over-grazing by 'released' populations of ungulates.

MANAGEMENT FOR A HEALTHY ELEMENT

Wolves in BC are the focus of a significant research and management efforts at this time. Localised monitoring of populations occurs, typically when there is a management focus (e.g. mountain caribou concerns, or managing for hunting prey species). However, the specific management goals for wolf populations should be considered within the realm of their functional role in different communities.

The Kuskwa-Kechika area of northeastern BC is the largest wilderness area in the rocky mountains. This area is world-renowned for having a completely intact predator-prey ecosystem and as such, wolves in this area are an important element of a unique ecosystem.

UNCERTAINTIES AND DATA GAPS

We note that in this example, a relatively common large predator is identified as having a potentially large functional role. The specific outcomes resulting from either significant population declines, or increases, will vary with the specific ecological context. This role could likely be ascribed to other large predators, such as grizzly bears, however we chose gray wolves as the focus because of their high biomass and their management status which seems to focus on them often as a 'pest' species to manipulate in order to obtain some kind of desired outcome in some other species. The effects of isolated management strategies that focus on an

outcome for a prey species may fail to adequately incorporate the functional role played by wolves in the different ecosystems of BC.

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2.2. KEY TERRESTRIAL SPECIES: NORTH AMERICAN BEAVER

WHY IS THIS SPECIES IMPORTANT?

The North American Beaver (*Castor canadensis*), above practically all others, is the most widely cited as an actual 'keystone' species in the scientific and popular literature. Using the systematic approach of examining function within the 'key functions' database for the Columbia Basin (Pandion 2001) it is the only vertebrate species which has the function of impounding water (see Section 1.6), and has been shown experimentally through large-scale removal experiments to act as a true keystone species in wetland / terrestrial interface communities. As a result of this action, the beaver effectively changes the course of succession, and has vast influence on ecosystems, species and habitats.

Functional Role: this rodent is unique in its ability to chew down significant numbers of trees and shrubs, and use them not only as a food source but in engineering dam construction which can flood or maintaining flooding in significant areas.

Impoundment by beavers can create wetlands and wet meadows. Beaver dams represent the only biotic method of establishing such wetland areas. There are then the many cascading impacts of wetland creation – habitat created for other species which may help to maintain the wetland (e.g. reeds/ rushes), flooding and killing standing trees which provide habitat for many cavity-nesting species and foragers.

In the longer term, as wetlands silt up highly productive meadows can form which ultimately become highly productive riparian habitat. The process of damming also has hydrologic implications including reducing channel scouring, reducing erosion locally, changing sediment loading downstream, changing flow regimes downstream. The influence of beaver dams on the water table also recharges groundwater levels, and can create cold springs resulting in better conditions for cold water fish species such as trout.

In the 'key ecological functions' database for the Columbia Basin, the beaver has a large number of relationships (Table X), one of which is exclusive (7 and 7.1), and others which only 3 species are noted as contributing to (e.g. 8 – to create standing dead trees).

Table 3. Functional roles of the beaver. Only this species has the role outlined in number 7.1 – impounds water. From Columbia Basin functional dataset based on Marcot (Undated).

Code	Functional Role
1	Trophic relationships
1.1	heterotrophic consumer
1.1.1	primary consumer (herbivore) (also see below under Herbivory)
1.1.1.1	foliovore (leaf-eater)
1.1.1.11	aquatic herbivore
1.1.1.13	bark/cambium/bole feeder
1.1.1.3	browser (leaf, stem eater)
1.2	prey relationships
1.2.1	prey for secondary or tertiary consumer (primary or secondary predator)
2	aids in physical transfer of substances for nutrient cycling (C,N,P, etc.)
3	organismal relationships
3.11	primary burrow excavator (fossorial or underground burrows)
3.11.1	creates large burrows (rabbit-sized or larger)
3.13	creates runways (possibly used by other species)
3.6	primary creation of structures (possibly used by other organisms)
3.6.3	aquatic structures
4	carrier, transmitter, or reservoir of vertebrate diseases
4.1	diseases that affect humans
5	soil relationships
5.1	physically affects (improves) soil structure, aeration (typically by digging)
7	water relationships
7.1	impounds water by creating diversions or dams
8	vegetation structure and composition relationships
8.1	creates standing dead trees (snags)

Research into the small-scale effects of the beaver has suggested functional influence down to very small scales, including the hypothesis that beaver herbivory on cottonwood has direct influences on a leaf-galling sawfly, which itself is proposed as a lower level keystone species (Bailey and Whitham 2006).

Functional Exclusivity:

As outlined in Table 3 above, this species is the only one that is highlighted as impounding water by creating diversions and dams. It therefore has a unique role and either removal or addition of a population in particular area will often have profound changes in habitat types available in an area.

Status and potential for future change:

Across continental North America the range of the beaver is considerably smaller today than historically, and the species has been extirpated from many regions.

In BC, this species is not considered at risk however the habitat of the beaver - wetlands and free-flowing rivers - have been extensively impacted throughout lower elevations particularly

in the south and southwest of BC. Hydroelectric impoundment, rural and agricultural development have all impacted historic habitat and local populations have likely been extensively impacted in these areas. In addition, there are many anecdotal cases where local changes to beaver populations are observed, either through loss due to local hunting or where habitat changes have resulted in local extirpation.

In addition, BC is currently undergoing a massive development of small and medium sized creek systems for small-scale hydro projects. The potential impact on beavers and their associated habitats is unknown and unmonitored to date.

CONSEQUENCE OF CHANGE OR LOSS

Removing the beaver locally often results in loss of beaver dams in the short-time (unless they have been established for significant periods and are now maintained naturally) and subsequent loss of standing water, removal of habitat for the associated aquatic and terrestrial species, and significant changes in downstream hydrology.

This process will influence habitat availability for a large number of other animals, including terrestrial species (birds /mammals / amphibians) and many aquatic species.

Note that on Haida Gwaii, the introduction of the non-native beaver is also causing significant habitat degradation, to the extent that water flow has been reversed across some areas of Graham Island in the Queen Charlotte Lowlands. This negative aspect of introduced beavers is not discussed further here, but remains a reason for classifying them as a key element.

MANAGEMENT FOR A HEALTHY ELEMENT

Under natural circumstances, beaver populations undergo population fluctuations as food supplies vary within the flooded area, and so populations likely undergo natural fluxes across different parts of the environment. However, there has been a historical lack of appreciation for the value of wetland habitats and beavers themselves are still considered a 'pest' by many landowners and users.

Although we are not suggesting here that beavers overall are at risk in BC, there have been significant historic changes in their abundance and distribution as a result of damming of large and small rivers, plus agricultural development which has filled-in many wetland areas removing potential habitat.

An assessment of areas which have been most affected, and where restoration programs may be appropriate would be beneficial. Some of this work has been undertaken in local areas (e.g. there is an on-going assessment of the effects of dams on habitat types in the Columbia Basin J. Krebs pers. comm.), but this type of work should be undertaken more widely across BC.

Beaver management guidelines have been produced for some regions of BC, specifically for Vancouver Island to guide highways and other public works (MoE 1995). The extent to which these guidelines are followed is unknown (by this author).

It noted by an MoE publication that beavers are 'greatly under harvested' in BC – annual harvests during the 1980s have averaged only 16,000 pelts (MoE undated), which is estimated at 6% of the most recent beaver population estimate of 400,000 – 600,000 animals. Management of beaver populations should take into consideration their local functional importance since in many places they are the primary agent creating wetlands, which themselves are a key habitat.

UNCERTAINTIES AND DATA GAPS

- Undertake assessment of key areas to focus restoration attempts, including low elevation areas impacted by large dam developments, where historic wetland complexes have been lost, plus areas with significant agricultural / rural development where wetland areas have been filled in.
- Review the extent to which best management practices effectively maintain functional beaver populations. Work with private landowners in key areas (including compensation programs).

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2.3. KEY TERRESTRIAL SPECIES: RED-BACKED VOLES

WHY IS THIS SPECIES IMPORTANT?

The Southern red-backed vole (*Clethrionomys gapperi*) was chosen as an example 'key element' because it has the potential to functionally influence a wide range of other elements of biodiversity, and has been suggested as a keystone element in forests of BC (Huggard et al. 2000). However, it may not meet the criteria as being under threat because, within its habitat, it is likely secure. At the landscape scale however, loss of old growth forest will cause significant changes in population abundance and distribution of this species. We include it as an example on this basis, because it provides some insight as to the range of potential changes that may occur as coarse filter elements such as old forest are significantly reduced across the landscape.

Functional Role:

This herbivorous rodent – is suggested as a key element because the species has known multiple functional roles in older forest communities, which include:

- being a significant food source for higher trophic species (including old forest associated medium mammals, plus forest hawks and owls),
- dispersing a significant volume and diversity of fungal species (e.g. more than 23 genera of fungi were identified as eaten by Maser and Maser 1988); these fungi have multiple roles including many being mycorrhizal fungi which increase nutrient availability for plant

species symbionts¹⁴, so maintaining overall productivity, and decay fungi which breakdown coarse woody debris,

- causing aeration of the soil through tunnel digging,
- at certain population densities can have sufficient influence on local mortality (due to foraging on roots of saplings and small trees) to cause local heterogeneity in the stand, increasing the number of niches available within the stand, and possibly contributing to the overall 'old-growthness' of the stand.

A number of different element of this cascade could be identified as the 'key', for example the fungi themselves, or coarse woody debris could be key elements, but red-backed voles are midway down the trophic level and so they play multiple function roles both up and down through the trophic levels.

Functional Exclusivity:

The functional exclusivity of this species to the roles outlined above is largely unknown. There are certainly other small mammals that inhabit both old forests and the community may shift to being dominated by peromyscus species in younger forests. The extent to which roles are transferable is unknown.

Status and potential for future change:

No provincial population status information exists for this species. However, it is primarily associated with old growth and mature forests (Clarkson and Mills 1994; Nordyke and Buskirk 1991), which are being reduced in distribution in many areas of BC. Populations of voles decline significantly with clearcutting, but can be maintained through partial harvest that retains canopy and sufficient brush cover. The potential for landscape level redistribution as a result of significant loss of old forest is therefore likely, particularly in areas with extensive clearcut harvesting. There are potential concerns at two different timescales: locally, as old-growth forest is replaced by young seral forest, and over the long-term as the extent of coarse woody debris over the landscape is reduced in size and abundance. The species is known to be associated with stands that have higher density of large pieces of coarse woody debris, and higher densities of 'truffles' (edible underground fungi; Hayes and Cross 1987).

Overall, at the landscape scale, across the province, loss of old growth forest will be likely to cause significant changes in population abundance and distribution of this species.

CONSEQUENCE OF CHANGE OR LOSS

As outlined above, the functional significance of the species is extremely varied. The potential changes of losing it from a significant portion of the landbase are therefore also enormous. As outlined below, it is extremely difficult to ascribe the 'driver' in these changes although in this case it is likely the driver is linked to 'old forest' loss. However, potential impacts from landscape level loss of the species include significant reduction in dispersal of fungi, resulting in potential decreases in both decay of coarse woody debris (itself a key element), and nutrient cycling (itself a key process).

The species is distributed through much, if not all of BC, and it is proposed that its loss from a landscape would be most significant

¹⁴ mycorrhizal are typically in a symbiotic relationship with rootlets of plants. Has been estimated that 85% of plants depend on mycorrhizal relationships with fungi (Kirk et al. 2001). This relationship may have significant consequences in nutrient poor environments.

- in large areas with extensive clearcut harvesting, and / or significant loss of understory species after harvest
- in areas of low productivity, where a reduction in mycorrhizal fungi and or decay speed, may have a significant influence on the vegetation community.

MANAGEMENT FOR A HEALTHY ELEMENT

Coarse filter assessment of availability of old growth is likely the most efficient approach to considering areas where loss of this species may be important. The effects of short rotation forestry will likely result in loss of this species from certain portions of the landbase. The ability of other small mammals to perform the same functions is unknown.

UNCERTAINTIES AND DATA GAPS

There are many uncertainties associated with identifying this species as a key element, including:

- the extent to which its functions are replaced in younger seral stands by other small mammal species.
- the influence of population cycles on function. It is possible that population cycles may reduce the dependence of any particular community to the functions played by the species.
- How loss of coarse woody debris across the landscape, as stands mature into future rotations will influence the ability of older stands to maintain populations of this species (and the associated fungi and other species).

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2.4. KEY TERRESTRIAL HABITATS: COTTONWOOD ECOSYSTEMS

WHY IS THIS HABITAT IMPORTANT?

Functional Role:

This ecosystem has many functional roles, including:

- providing relatively rare deciduous habitat for a large number of species. The cottonwood tree itself is prone to limb breakage and often creates large natural cavities for nesting.

In addition, many primary and second cavity nesting species use the tree for habitat. It has been suggested to be the most important tree species for cavity nesters in British Columbia.

- Cottonwood ecosystems tends to be located adjacent to water bodies (though not always). Because of this position, at the interface of the terrestrial and freshwater aquatic, it often provides habitat for a large diversity of other species, including nesting habitat for species requiring large trees close to water (e.g. great blue herons, bald eagles), many owl species, black bears and other species foraging on salmon streams.
- Large size, and relatively short longevity of the species means it likely contributes significantly to riparian functioning, including creating habitat for fish spawning (and other aquatic breeding species) through creates of pools,
- Ecologically it tends to include a diversity of plant communities that have relatively limited distribution across the landbase, including a number of listed plant communities including 10 red-listed and 3 blue-listed plant communities (CDC species explorer) which are associated with a wide diversity of biogeoclimatic subzones and site series that span the province.
- This ecosystem contributes to the structural integrity of streambank / lake shore habitats. In many locations cottonwood ecosystems exist within the flooding zone of streams, rivers and lakes.
- This species (along with trembling aspen) is hypothesised to act as a nutrient pump in forested ecosystems. Nutrients transported by these species into the canopy are released and made available to support other species, such as cyanobacteria found in greater numbers in areas where nutrients are made available from this 'drip zone' effect (Arsenault and Goward 2000). This function in itself has been suggested as rationale to describe cottonwoods and aspen as keystone species in BC.

Functional Exclusivity:

There are relatively few deciduous trees in BC, and their distribution is relatively limited. Many of the bird species associated with this ecosystem will use other trees as nesting habitat, but cottonwood ecosystems themselves have a very high density of use as a result of the characteristics of the tree itself and its distribution adjacent to water bodies. Groups of aspen in some ecosystems may play a similar role, but are less associated with water. The functional exclusivity of this species is therefore likely quite high.

Status and potential for future change:

No specific distribution information is available for this ecosystem. However, cottonwood ecosystems have been identified from a number of reports as being at threat across the province, due a number of different impacts (Holt 2001; Holt et al. 2003). Direct loss of this ecosystem has resulted from damming of rivers which has flooded areas that were historically dominated by cottonwood ecosystems and in some cases this represents a significant impact on the extent of the entire ecosystem (Mackillop 2006 in prep.), plus loss of trees or whole ecosystems through rural or recreational development and agriculture. In addition, regeneration of the species and therefore the ecosystem has been reduced in many areas because of reduced water levels and reduced flooding potential around many lakes (e.g. around the West Arm of Kootenay Lake) since this species regenerates primarily after flooding. Climate change also has the potential to influence the distribution of the species, perhaps through the

significant change expected in frequency of low flows and reduction in peak flows (see freshwater section).

Relevance in BC:

This tree species occurs throughout much of British Columbia. Its importance as habitat is high across the whole province, though its exact functional role and exclusivity will change in different areas of the province. On the coast some functions can be taken by red alder, and in areas where there are significant stands of birch or aspen, these species may be able to fulfill some functions. However, cottonwood, because of their size remain a very important species across the range of their distribution.

CONSEQUENCE OF CHANGE OR LOSS

Loss of this habitat has the potential to influence the populations of a wide range of species. The habitat was formerly distributed throughout the whole of BC, and as stated above, tends to be associated with riparian zones. Because the replaceability of the ecosystem tends to be low, the expected impact of loss of this ecosystem is likely to be high, and impacts would include:

- Loss of breeding habitat for a significant number and diversity of species
- Loss of already listed plant communities
- Loss or decline in quality of fish and other aquatic species' breeding habitats
- Loss of structural integrity of hydriparian zones, resulting in loss of within-stream habitat, bank stability, increased sedimentation etc.

MANAGEMENT FOR A HEALTHY ELEMENT

This species is mapped on forest cover maps, but the distribution of the broader riparian ecosystem is not systematically monitored in BC. However, as inventories are updated (and site series mapping becomes more generally available), it would be possible to monitor the historic impacts on crown land.

However, many cottonwood ecosystems exist on private land, and here there is no consistent mapping and no way to assess trends through time. In some local areas, specific impacts have been monitored (e.g. in the Columbia Basin a project has been underway to quantify the effects of flooding to create dams. This project identifies one of the major impacts to have been loss of cottonwood ecosystems. Mackillop 2006 in prep.).

UNCERTAINTIES AND DATA GAPS

Where it occurs at low elevations, likely a significant area of this ecosystem occurs on private land. In these areas distribution mapping is even weaker than on crown land. In addition, the impacts are likely greater as historically wetter areas are maintained as agricultural land, or developed. No regulations occur to prevent complete loss of these important ecosystems on private land.

Damming of rivers has had a significant negative impact on the distribution of cottonwood ecosystems in BC. In addition, regulation of flooding by dams reduces the wetland ecosystems often associated with cottonwood ecosystems. Although this is generally known, management of water levels rarely incorporates objectives for maintaining ecosystems or other biodiversity values. The overall impacts of damming are therefore generally unquantified and may represent a significant threat to remaining mature cottonwood ecosystems.

Historic losses of this ecosystem have likely been significant (from the variety of sources outlined above). Although some regions have examined the specific losses occurring from

individual developments (e.g. specific losses from dams in the Kootenay region; Mackillop 2006), a strategic restoration plan is needed to prioritise the highest biodiversity areas for and areas with highest losses, for restoration.

The ecosystem has the potential to be impacted by climate change, as flow regimes and therefore flooding are reduced (see aquatic section on increased low flows). Although not completely dependent on regeneration under flooded conditions, this species preferentially does regenerate under these conditions. Climate change may therefore exacerbate already marginal conditions for regeneration. An assessment of management options to maintain these ecosystems in highest priority areas is required for the province.

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2.5. KEY TERRESTRIAL HABITAT/ ECOSYSTEM: WETLANDS¹⁵ IN DRY ECOSYSTEMS

WHY IS THIS HABITAT IMPORTANT?

Functional Role:

Wetlands in general are known to be extremely high in terms of biodiversity values: they provide habitat for both a large species richness and are often associated with a relatively large number of listed species (Gregory et al. 1991; Machmer et al. 2004). In the southern portion of British Columbia (the south Okanagan in particular, but including the southern portion of the Kootenay trench and the East Kootenay trench, plus the lower Fraser valley) they are particularly important because they are situated in dry environments, making the water resource itself and habitat values provided of higher overall importance since the distinction between the habitat and surrounding upland is more pronounced. There are a number of different types of 'wetlands', which have their own unique biodiversity values and issues.

Functionally, wetlands:

- Provide habitat (breeding and non-breeding) for a large number of both freshwater aquatic and terrestrial species. Although important in all areas, their importance is amplified in dry environments highlighted here, since water resources are generally limiting. Habitats are both 'terrestrial' and 'aquatic'. On the aquatic / terrestrial interface they provide a high diversity of niches, including habitat such as cottonwood habitats (see key habitat), habitat

¹⁵ Wetlands are areas where soils are water-saturated for a sufficient length of time such that excess water and resulting low soil oxygen levels are principal determinants of vegetation and soil development. Wetlands will have a relative abundance of hydrophytes in the vegetation community and / or soils featuring 'hydric' characters. From MaxKenzie and Moran 2004.

for terrestrial species such as turtles or many birds which use the water resource but breed on land. Functions of submerged habitat include providing habitat for invertebrate species, providing food / shelter for fish, oxygenating water sources, recycling nutrients and filtering heavy metals. An example of an important invertebrate group that is affected by the removal or degradation of wetlands are dragonflies and damselflies (Odonata). These species inhabit a variety of different types of wetlands (e.g. small lakes and ponds, alkaline lakes, ephemeral ponds, sedge marshes, springs and shallow seeps, and the community composition of Odonata differs in these different habitat types (Cannings et al. undated). Because these species are often the top predator in the invertebrate community, loss of some of these species could result in similar cascades to those predicted by loss of large vertebrate predators (e.g. see wolves as key element).

- Provide habitat for a large number of listed species;
- Provides 'stepping stones' for dispersal of many of the species limited to these habitats, allowing dispersal or colonisation of areas;
- Provide water filtration and storage, providing seasonal sources of water in otherwise water limited environments;
- Reduce soil erosion, and filter sediment or other pollution;
- Influence nutrient cycling;
- Undergo succession following hydrologic disturbance that can result in alternative climax communities – these patterns increase habitat diversity at the landscape scale.
- Provide storage and filtration for water supplies to the broader landscape (for human and non-human usage).

Functional Exclusivity:

For many species, wetlands provide the only available breeding habitat, and because they are a generally scarce resource, loss of even a small number of wetlands can significantly impact species diversity and functions.

Status and potential for future changes:

Wetlands globally and across Canada are known to be at risk. In Canada, wetland area has decreased by 15% since European settlement (referenced from MacKenzie and Shaw 1999). This is particularly significant since Canada is estimated to hold about 24% of the global distribution of wetlands.

In BC, patterns are similar and there have been and remain many threats to wetland habitats; it has been estimated that 30% of all land developed rurally between 1967 and 1982 was wetland habitat (Sandborn and Penfold 1996). These impacts include agricultural development, hydrologic modification, hydroelectric development, grazing, forestry, urbanisation / rural development, and invasive species (MacKenzie and Shaw 1999). Wetlands have been significantly impacted by development of low elevation private land, and in the southern Okanagan in particular are impacted by the suite of potential threats outlined above.

Climate change will no doubt have an impact on the distribution and functioning of wetland ecosystems, depending on how they are maintained, and their location. The impacts of climate change in these already dry ecosystems may be particularly pronounced.

Relevance in BC:

Wetlands are of importance ecologically across BC. However, the wetlands associated with the more arid central and southern regions of BC are highlighted here because a) the level of biodiversity values and uniqueness associated with them is very high and b) because the losses in these areas have historically been high and continue today due to extensive rural development in these ecosystems.

CONSEQUENCE OF CHANGE OR LOSS

Loss of breeding habitat for a high number and diversity of habitat clearly has the potential for significant population consequences for many species, and their associated functional species. An example of the type of cascading impacts that could occur from wetland impacts is loss of dragonfly species which are aquatic breeders. As a top predator in the invertebrate world, loss of this species could be hypothesised to have as significant a level of impacts (though at a smaller scale) as removal of wolves. Alternatively, wetlands also provide habitat for many species at the bottom of the food chain (e.g. mosquitoes) without which many higher level species can be impacted (equivalent to the loss of ungulates on higher level predator populations).

The listed status of many wetland-associated species is likely a direct result of the loss of wetlands themselves; i.e. the effects of wetlands are already seen through the number of listed species associated with them.

MANAGEMENT FOR A HEALTHY ELEMENT

A wetland classification system (the wetland and riparian ecosystem classification project) has been developed for British Columbia (Mackenzie and Moran 2004). This is the first step allowing a tracking process to map the trends for different wetlands.

In some areas, wetland mapping including consideration of historically degraded wetlands, has taken place. For example, the Columbia Basin Wildlife Compensation Program has undertaken historic mapping and an assessment of values lost by inundation due to dam building (J. Krebs pers. comm.; report in prep). This type of assessment should be undertaken in all areas where significant development and loss of wetland habitats has occurred. Extensive mapping and analysis of this kind can help in the development of appropriate restoration and management strategies for wetlands across these vulnerable zones. The site associations used in the wetland classification system can be used to guide restoration activities.

In addition, the wetland classification system is intended to highlight wetlands of particular importance to biodiversity, and should be used in this way to identify key remaining wetlands in order to guide protection both on crown and on private land.

UNCERTAINTIES AND DATA GAPS

There is currently no strategic assessment of key wetland areas for protection, and restoration. At minimum this should include

- Identification of particularly high potential biodiversity wetlands (the classification system should help with this process).
- Location of key areas for restoration (requires analysis of impacts and opportunities), plus partners to link in private land areas.
- Reliable mapping is generally limited. Products that are used to infer wetlands (e.g. TEM / TRIM) often are mislabeled, because wetlands were not the focus of that work.
- Identify and quantify very small wetlands since these are suggested to be particularly key to maintaining biodiversity values across the landscape (Semlitsch and Bodie 1998).

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2.6. KEY TERRESTRIAL HABITAT: BROADLEAF TREES

Broadleaf trees refers to the general category including red alder (*Alnus rubra*), trembling aspen (*Populus tremuloides*), paper birch (*Betula papyrifera*), and black cottonwood (*Populus trichocarpa*). 'Cottonwood ecosystems' themselves are identified as a key habitat, but in this category the focus is more generally broadleaf trees distributed either in groups or singly distributed throughout the forested zones of British Columbia throughout BC, not necessarily associated with water.

WHY IS THIS HABITAT IMPORTANT?

Functional Role:

- Trembling aspen and paper birch are associated with soil microbes and ectomycorrhizal¹⁶ networks that link broadleaves and conifers in mixed forests. When deciduous species are present carbon transfer and nitrogen fixation are increased. These effects are seen at the seedling stage and although there is competition between the broadleaf species and Douglas fir, over the long-term it is suggested that the broadleaf species are an essential component of maintaining longer term ecosystem productivity (Simard and Vyse in press; Sachs 1996) because of the increased diversity of fungal networks resulting in increased nitrogen inputs.
- In general, broadleaf trees have the highest breeding use of any trees. They are used as breeding habitat for a wide range of bird species (primary and secondary cavity nesters), plus as mammals such as squirrels and flying squirrels. In general, they provide habitat for the small to mid-sized species, but do not generally become large enough to provide significant habitat for the largest species in these categories (e.g. pileated woodpeckers or large mammals).

¹⁶ A mycorrhiza (typically seen in the plural form mycorrhizae meaning "fungus roots") is a distinct type of root symbiosis in which individual hyphae extending from the mycelium of a fungus colonize the roots of a host plant. Different sorts of fungal structures are found in mycorrhizal trees and in roots of most herbaceous plants.

- They also provide important foraging habitat for many birds and mammals, and therefore presumably for a wide diversity of non-vertebrate species.
- They are known to prevent the spread of *Armillaria ostoyae* root disease among conifers (Gerlach et al. 1997) and also reduce attack by weevils and spruce budworm (a growing forest health agent in BC's forests, possibly being exacerbated by climate change).
- They also increase productivity of soil directly by infusing large volumes of litter into the system annually.

Functional Exclusivity:

Many other tree species can provide the types of habitats found in broadleaf trees. However, many studies have shown a preference for these trees, and the density and diversity of habitats provided by them exceeds almost all other tree species. In some areas trees such as western larch can provide a similar diversity of breeding habitat.

We do not have any information on the exclusivity of the foraging opportunities provided by these species, but suspect they are relatively exclusive, since there is such high use.

The ecological importance of these individual species is known, particularly in the interior cedar hemlock zone (for paper birch and trembling aspen), and in coastal ecosystems (for red alder).

Status and Potential for future changes:

No population or distribution information is available provincially for these species. However, because they are relatively short-lived, it has been suggested that much of the mature deciduous component is being lost from the BC landscape as a result of a combination of removal from private land and forest harvesting (S. Simard pers. comm.). In addition, the combination of management of clearcuts (extensive brushing and chemical removal of deciduous species) combined with fire suppression across the broader landscape is resulting in lack of a recruitment cohort both within and outside the managed forest landscape (S. Simard pers. comm.). It is hypothesised that the existing mature cohort, between 100 – 150 years in age, is close to its natural longevity, and there is very little recruitment in some areas.

Relevance in BC:

These species, as a group, are distributed throughout the forests of BC. Although much of the research has occurred in the productive interior cedar hemlock forests it is likely that these effects are equally important in other ecosystems and perhaps more so in less productive ecosystems where nitrogen deficiency may be increasingly important. A recent paper highlights how forest management strategies tend to result in extensive removal of these species across much of the interior cedar hemlock zone (Simard and Vyse 2006 In press)

CONSEQUENCE OF CHANGE OR LOSS

In the short-term, loss of a mature component of broadleaf species will result in significant loss of habitat for a wide diversity of species, some of which could be keystone themselves, including the diversity of woodpecker species and their associated secondary cavity nesters.

In the longer term, loss of these species from regenerating forests (managed and natural) may have significant productivity impacts due to reduced nitrogen fixation from the diversity of mycorrhizal fungi another species which could be classified as a key functional species.

MANAGEMENT FOR A HEALTHY ELEMENT

Management strategies that promote or maintain forest diversification as opposed to forest simplification as promoted by current forestry management strategies would provide for a

regeneration cohort of these species throughout the managed forests of BC (Simard and Vyse in press). More detailed strategies for meeting these goals are suggested in Simard and Vyse in press).

UNCERTAINTIES AND DATA GAPS

Inventory of these species in BC, which have typically been considered non-commercial, is weak. The last inventory in the province was undertaken in the early 1990s, and a new inventory is underway. This process may be used to identify areas of particular concern where updated management strategies should be employed.

Sufficient science exists around the functional importance of these species, however the new knowledge is slow to be incorporated into management practices.

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2.7. KEY TERRESTRIAL PROCESS: CYANOLICHENS AND NITROGEN FIXATION

Lichens are obligate mutualistic associations between a fungus and a photosynthetic partner and for 'cyanolichens' cyanobacteria are the partner. As a result, cyanolichens 'fix' nitrogen making otherwise inactive nitrogen available to the ecosystem. Cyanolichens are estimated to comprise about 50% of the epiphytic macrolichens in BC (Arsenault and Goward 2000b). Conifers belonging to the Pinaceae provide habitat, in coastal regions, for at least 43 cyanolichen species, 12 of which occur exclusively on conifers. Hardwoods support a similar number of cyanolichens but provide exclusive habitat for only four species. Cyanolichen diversity on conifer branches is shown to increase along a gradient of increasing summer precipitation (Goward and Arsenault 2000a).

Specifically for BC, 31 epiphytic cyanolichens are known, including 12 species that are rare within the province as a whole (Goward and Arsenault 2000). Maximum diversity is found in lowland old-growth rainforests, established over nutrient-rich soils, which tend to be restricted to toe-slope positions in the wettest subzones of the Interior Cedar-Hemlock BEC zone. These areas are noted as supporting "one of BC's richest assemblages of rare cyanolichens but also representing one of the province's rarest and most endangered forest ecosystems" (Goward and Arsenault 2000).

In addition, a very high diversity of cyanolichens have been found in riparian forests (in western Oregon – Peterson and McCune 2003), and hardwood trees found in these areas may be particularly important for maintaining diversity and productivity of these ecosystems. Riparian associated species are vulnerable to loss of these species due to reduced flooding events, selective impacts on private land at low elevations (see other key elements highlighted in this paper).

The likely occurrence and diversity of cyanolichens in a forest can be predicted by considering a set of key factors. In decreasing order of importance these are: air quality, climate, elevation, soil nutrient status, forest age, proximity to deciduous trees, soil moisture, and stand spacing (Goward and Arsenault 2000b).

Note that individual species could have been chosen under the key species, but the key element of interest is the nitrogen-fixing process that all cyanolichens undertake.

WHY IS THIS PROCESS IMPORTANT?

Functional Role:

As a group these species are functionally important because:

- They have a key functional role of fixing atmospheric nitrogen, so making that resource available to both the lichens themselves, and the broader ecosystem. This is particularly important in many forests in BC because they tend to be nitrogen-limited (G. Utzig pers. comm.).
- Additionally, this diverse group provides a variety of structural elements within the stand. As a result this group greatly increases the diversity of structural niches available in the stand and are known to be associated with a diverse array of invertebrates. This function is not limited only to cyanolichens but to the broader array of lichens.
- The invertebrate diversity associated with lichens provides food sources for resident and migrating birds that are higher than those observed in second growth forest (Drapeau et al. 2003; Patterson et al. 1995).
- It is hypothesised that the increased moisture retention associated with lichens in old growth forests may act to reduce fire hazard in these stands (Slack 1988).

Functional Exclusivity:

Other groups can fix nitrogen (e.g. bacteria associated with root nodules) but the location of cyanolichens makes them relatively rare, and therefore likely to be functionally quite exclusive.

Status and potential for future changes:

No population or range information is available provincially for these species. However, many of these cyanolichens are restricted to, or are most abundant in, old-growth and mature forests (Richardson and Cameron 2004; Radies and Coxson 2004; Price and Hochachka 2001). Studies that examine the effects of partial harvesting or young seral stage suggest that recolonisation by many of these species is very slow (in excess of 140 years), and requires very high levels of stand retention for rapid recolonisation (Price and Hochachka 2001). As a result, populations of these species are highly vulnerable to short-rotation forestry practices as currently practised in the majority BC's forests.

Many of these old-growth forest lichens take many centuries to build up a significant biomass, even though colonisation may begin at an early age (McCune 1993; Peck and McCune 1997). Even natural gaps of 1-3ha more than 100 years old, have been shown to have depauperate communities of these lichens (Benson and Coxson 2002). Similarly, other species have been shown to respond poorly to edge effects caused by clear-cuts or partial harvesting (Sillett et al. 2000). Retention of higher levels of the stand has been shown to be more successful in maintaining the lichen community – for example maintaining 70% of the forest in the ESSF did not alter lichen presence in the remainder of the stand (Coxson et al. 2003). Other studies have shown that recolonisation of a stand may not really occur until a minimum of 110 years old, however short rotations may prevent significant parts of the landscape from attaining this relatively young age in future.

CONSEQUENCE OF CHANGE OR LOSS

- The importance of these species is widely known, and the potential loss of them as a result

of forest management practices is also noted. However, the long-term effects of losing significant diversity of nitrogen-fixing species in forested ecosystems is largely unknown.

- These ecosystems tend to be nitrogen limited, so it can be assumed there would be a concomitant reduction in productivity. Long-term effects are completely unknown.

MANAGEMENT FOR A HEALTHY ELEMENT

- Ensuring adequate protection of representative old forest, in particular low elevation high productivity stands in the Interior Cedar-Hemlock zone (as highlighted by Goward and Arsenault 2000a). This is currently not achieved by the coarse filter management strategy employed by the Province of BC.
- Ensuring a range of stand level retention occurs, with examples of high retention to ensure that these species are maintained across at least part of the timber harvesting landbase.
- Where ecologically appropriate, employ longer rotations, allowing development of full communities of lichens across time and space.

UNCERTAINTIES AND DATA GAPS

Additional research is needed to fully understand how this suite of species influences broader forest ecosystem functioning. Mapping of distribution of species and communities and basic natural history information would improve this understanding at the most basic level.

The response of the whole group to forest harvesting is largely unknown, though in general they are intolerant to disturbance and take significant periods of time to recovery abundance and diversity.

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2.8. KEY TERRESTRIAL PROCESS: FAUNAL PEDOTURBATION

It has been suggested (Marcot Undated) that identifying the key ecological functions of the full suite of species in an ecosystem can be used to identify potential 'key species' for management.

As highlighted in the Methods (Section 1.6) in this paper, species that have a large number of functions, or have exclusive functions not played by many other species have a higher probability of being strong interactors. The Key Ecological Functions database for the Columbia Basin (Pandion 2001) has been compiled and we used it here to examine its utility in identifying individual species, or groups of species which play key ecological roles (see Methods).

Within the Columbia Basin only 29 species are highlighted as 'physically affecting soil structure and aeration typically through digging'. Of these, the vast majority exist in the dry zones in the valley bottoms in the Interior Cedar-Hemlock, Interior Douglas-Fir and Ponderosa Pine biogeoclimatic zones. Of these low elevation species a fair number of them are considered rare or threatened (Table 4).

Table 4. Species identified as physically affecting soil structure and aeration typically through digging, in the Columbia Basin.

Species Identified as affecting soil structure	Ranking
Tiger Salamander	Red
Long-toed Salamander	Yellow
Great Basin Spadefoot	Blue
Western Toad	Yellow
Pygmy Short-horned Lizard	Red (apparently extirpated in S. BC)
Western Skink	Blue
Rubber Boa	Yellow
Gopher Snake	Red
Burrowing Owl	Red
Belted Kingfisher	Yellow
Shrew-mole	Yellow
Nuttall's (Mountain) Cottontail	Blue
Snowshoe Hare	Yellow
White-tailed Jackrabbit	Red
Least Chipmunk	Yellow / Red
Yellow-pine Chipmunk	Yellow
Woodchuck	Yellow
Yellow-bellied Marmot	Yellow
Hoary Marmot	Yellow
Columbian Ground Squirrel	Yellow
Golden-mantled Ground Squirrel	Yellow

Species Identified as affecting soil structure	Ranking
Cascade Golden-mantled Ground Squirrel	Yellow
Northern Pocket Gopher	Yellow / Red sub-species
Great Basin Pocket Mouse	Blue
Beaver	Blue
Deer Mouse	Yellow
Bushy-tailed Woodrat	Yellow
Water Vole	Yellow
American Badger	Red

WHY IS THIS PROCESS IMPORTANT?

Functional Role:

- Pedoturbation (though various forms) is a critical part of maintaining soil functions. Some key soil functions include to a) sustain biological productivity, activity and diversity, b) store and cycle nutrients, c) partition water, energy and solute flow, d) filter and buffer organic and inorganic material and e) support above-ground structures (list adapted from Meurisse 1999).
- As a group, the species listed above all contribute to pedoturbation by digging tunnels / burrows and foraging in the soil. This mixing is important because it breaks up soil fragments, breaks up soil horizons, and increases productivity as a result. It also potentially changes water flow through soil, creates bare ground for succession to occur, and can be a significant aspect in soil formation itself.
- In addition, some species have a broader function in providing specific habitat for other species (e.g. burrowing owls / rabbits / badgers) which create burrows that are later used by other species.
- Soil micro-organisms play crucial roles in soil functioning, and their abundance and diversity within soil can be related to its physical structure. Loss of key mixing agents may therefore have an impact on these species, and have significant cascading impact on overall soil function.

Functional Exclusivity:

- In this case an otherwise unrelated group of species were identified because as a group they create the biotic component of soil pedoturbation.
- Other elements also cause such mixing, including the physical effects of freeze/ thaw processes and changes in humidity, especially in clay soils.
- As outlined in the Methods, this database includes only vertebrates, so key species missing from this list include earthworms, ants and many other invertebrates.

Status and potential for future population changes:

- No population information is available for the broad suite of species responsible for this process.
- However, a significant number of the vertebrate species that live at low elevation are identified as having a significant role in pedoturbation are red or blue-listed in BC. Many of these species have limited range compared to their historic distribution due to extensive ruralisation of low elevation in the ICH, IDF and PP.

Relevance in BC:

- This factor is potentially relevant to all areas in BC since biotic agents are active throughout the region. However, the ecological consequences of removal will vary by specific region (i.e. what species are present), and soil types.
- Low elevation ecosystems were prioritised here because they have a significant number of biotic agents and so their overall effect is likely to be large. It is unknown whether there are particular ecosystems in BC where a single biotic element has an irreplaceable role. This may be true in the creation of habitat but is unlikely from a soil mixing perspective.
- A number of studies have suggested biotic pedoturbation has a higher level of importance in non-treed ecosystems, particularly in the alpine and in desert/ grassland ecosystems where abiotic disturbance processes such as freeze/ thaw, or high severity fires or local events such as trees-uprooting etc may be less relevant.

CONSEQUENCE OF CHANGE OR LOSS

Soil-mixing is a primary factor affecting species richness, diversity and maintaining normal soil functioning. It has the potential to influence successional pathways, vegetation dynamics, nutrient cycling and decomposition of above-ground elements so maintaining soil productivity.

From a habitat perspective, opening up the soil, and creating burrows is an essential aspect of maintaining species diversity and abundance since species which play this role are relatively limited in distribution.

A number of research projects identified larger mammals as very important ecosystem-specific elements, resulting in species such as pocket gopher being identified as 'keystone species' in a prairie ecosystem (E.g. Sherrod and Seastedt 2004).

The general process of soil disturbance has been identified as factor influencing whether the treeline can 'move' in alpine tundra ecosystems (Butler et al. 2004). This factor may be an important component of maintaining ecosystem resilience in the face of climate change.

In addition, loss of pedoturbation agents may have particular short-term significance in ecosystems where other factors are causing soil damage. For example soil compaction resulting from development, forestry or agriculture may have more significant long-term impacts on ecosystem productivity if the resilience of the soil is reduced.

MANAGEMENT FOR A HEALTHY ELEMENT

As outlined below, baseline data are lacking for many of these species. Gathering a systematic baseline distribution of these species, particularly those with a historically wide distribution and relatively high local abundance (e.g. least chipmunk), but which may be in localised decline as a result of rural or agricultural development would help to identify areas where significant changes may be occurring.

In addition, work has been undertaken in some areas to identify which soil types may be more or less resilient to external changes in western Washington (Szabolcs 1994 – from Meurisse 1999). Applying such a model to the soils of BC may provide guidance as to which areas are of high potential concern as a result of their inherent lack of resiliency.

UNCERTAINTIES AND DATA GAPS

Key uncertainties include the lack of research to identify which individual species (or groups of species) may be of higher importance in this role than others. This key element was identified using theory – i.e. the general importance of pedoturbation is known, and in the low elevation IDF / ICH / PP there appear to be a large number of faunal agents which likely affect pedoturbation processes. Many of these species are being reduced as a result of agricultural

or rural development. We can therefore hypothesise that these may be of high functional importance. However, the contributions of individual species to these processes are unknown.

Many of the lesser known species are likely affected by land use changes but are not monitored in any systematic fashion, and in fact their local distributions are often not clearly known (J. Dulisse pers. comm.). As a result, changes in population sizes and distributions for many of these species are unknown and no baseline data exists for them to be tracked.

The list of species for this factor was developed as a test case using the Columbia Basin species / habitat relationships database. This database focuses on vertebrates, and as a result, some key species which may have very high functional significance (e.g. ants – Lobry de Bruyn 1999) are not included, and other relevant species (e.g. alligator lizards) are simply missing from the list. Again, this highlights the lack of technical information available to systematically identify key species.

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2.9. KEY TERRESTRIAL PROCESS: INSECT POLLINATION

WHY IS THIS PROCESS IMPORTANT?

Pollination of plants occurs through both biotic and abiotic processes. A very wide range of animals provide pollination as a function, including bees, flies, moths, butterflies, beetles, birds and bats. However, insects are the primary pollinators in much of North America. Mutualisms between wildflowers and pollinating insects are often essential for both the effective reproduction of the plant and the pollinator.

Without pollination many species of plants could simply not reproduce since pollination is the process of transferring pollen between plants. It is estimated that approximately 65% of flower plants and some seed plants require insects for pollination. This percent is higher for economic crops.

Bees are particularly important pollinators, because they tend to be highly specialised, and they

visit high numbers of flowers at a time. Their pollen transfer efficiency is very high. As a result, the remainder of this discussion focuses on bees, but could be expanded as the available science becomes available.

The estimated value of this function in the US in relation to the production of human food, is estimated at 4-6 billion dollars annually. This direct estimate does not take into account the indirect benefits of maintaining broad ecosystem functioning by maintaining natural biodiversity (Losey and Vaughan 2006).

Functional Role:

- Pollination of a wide variety of flowering and seed producing plants.

Functional Exclusivity:

- Highly variable by species of plant.
- However, fewer exclusive relationships in the forests of BC than found in tropical forests, due presumably to the timeframe available for co-evolution.
- However, the suite of pollinator species may be similarly affected by land use and habitat changes. Exclusivity may therefore not be relevant.

Status and potential for future changes:

The extent to which pollinators are at risk is largely unknown for BC (E. Elle pers. comm.). However, in other parts of the world there are examples of individual pollinators and their host plants being severely impacted in their particular ecosystems (e.g. in Hawaii, eastern Canada, southern US).

In a review article focusing on the United States, it is noted that there is no evidence to suggest a drastic short-term decline in the insect pollinators overall. However, they also note that there is however a steady decline in insects associated with the overall decline in biodiversity, as a result of heavy degradation of ecosystems by humans (Kremen et al. 2002). A research example in California shows that European honey bees which have typically been introduced and managed as crop pollinators are declining in abundance due to a variety of diseases. Native bee communities have been shown to be able to provide a full pollination service, where farms are located close to high value habitat and when organic practices are used. However, other areas were experiencing both reduced abundance of honey bees and native bees, and in these cases economic losses were experienced due to crop failures (Kremen et al. 2002).

It has also been suggested that under some situations, the most important species are lost first (Larsen 2005). In two separate ecosystems the largest bodied examples (bees and beetles) were the most extinction-prone, and in both cases these species were also the most functionally important. Loss of these species therefore had a higher functional impact than random species losses on the remaining community.

In BC, research is underway in Garry Oak ecosystem (E. Elle pers. comm.; Garry Oak Recovery Team 2006). Some species of plants are 'obligate outcrossers' and require pollination in order to reproduce – and as a result may be particularly vulnerable to landscape changes that reduce availability of pollinators. And subsequently, pollinators that are tied to individual host plants for both rearing larvae and for nectar sources may show cascading effects leading to local crashes in this system. The extent to which this may be occurring with bees in the Garry Oak ecosystem is currently being studied (E. Elle pers. comm.).

Relevance in BC:

- Potentially highly relevant in BC due to high biodiversity, wide range of ecosystems, high number of rare plants and insects, particularly in areas such as the Southern Okanagan.

CONSEQUENCE OF CHANGE OR LOSS

- Unknown, but potentially loss of pollinator, associated plant species and cascading impacts through ecosystems.
- Extent possible here is unknown.

MANAGEMENT FOR A HEALTHY ELEMENT

There is relatively little research in this field, but a recent study suggested that there were some weak positive correlations between conservation planning per se (using the usual type of coarse filter, and fine filter indicators) and maintenance of broad ecosystem services including pollination (Chan et al. 2006). However, they also found that targeting biodiversity conservation plus consideration of key ecosystem services directly provided a more efficient approach to planning overall.

This subject has become a subject of interest in other areas, because recent papers have highlighted the potential economic implications of insects (Losey and Vaughan 2006). Other publications have also been produced (e.g. Shepherd et al. 2003) which may provide useful strategies for pollinator conservation (title unavailable to author).

UNCERTAINTIES AND DATA GAPS

A strategic assessment of areas of interest may be appropriate. For example, in the S. Okanagan where insect populations may have been significantly impacted by rapid agricultural development including extensive use of pesticides.

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2.10. KEY FRESHWATER SPECIES: ANADROMOUS SALMONIDS

Anadromous salmonids include several species of salmon, trout and charr that have an ocean-rearing life phase. Mostly these are the five eastern Pacific salmon species: chinook (*Oncorhynchus tshawytscha*), chum (*O. keta*), coho (*O. kisutch*), pink (*O. gorbuscha*) and sockeye (*O. nerka*). In addition, some trout and charr species have anadromous life history forms:

rainbow/steelhead trout (*O. mykiss*), coastal cutthroat trout (*O. clarki clarki*), and Dolly Varden charr (*Salvelinus malma*).

WHY IS THIS SPECIES IMPORTANT?

Functional Role:

The majority of freshwater systems in BC are oligotrophic, or nutrient-poor. This means that the inherent productivity of these water bodies is low and the abundance and biomass of fish that can be supported is also low. Anadromous salmonids act as a nutrient pump, by bringing nutrients from the ocean to nutrient poor interior waters. Anadromous salmonids hatch in freshwater streams (and occasionally lake littoral areas) and migrate to the ocean after a variable amount of time in freshwater. They grow and accumulate most of their somatic tissue in the ocean and return to natal streams and lakes to reproduce, where they die¹⁷.

Anadromous salmon may return in large numbers, and this returning biomass supports many terrestrial and aquatic species. Many adults are caught and consumed en route or on the spawning grounds, eggs are eaten by birds and fish, and carcasses of spawned-out salmon are a substantial input of nutrients to many freshwater systems (Cedarholm et al. 2000). When the young hatch the following spring and summer they are the prey base of many more species. Stream- and lake-rearing juveniles are often the dominant component of the fish community.

There is some potential for positive feedback between present and future salmon escapements, due to the profound nutrient inputs provided by returning adults (Wipfli et al. 1998, 2003). Lower returns lead to lower nutrient levels in lakes and rivers which in turn lowers freshwater carrying capacity and thereby the ability of a waterbody to support fish.

Functional Exclusivity:

There is clearly some redundancy in this element since it represents more than one species. But there are important differences in geographic range, run timing, and abundance patterns among these species, such that redundancy is far from complete. For example, niche separation is high both in freshwater and in the ocean—loss of one species of salmon is not “made up” by an increase in another. Returns in some rivers may be abundant for one species and not others, and geographic separation among species within the same river systems is also common.

To some extent species with adfluvial forms (e.g., bull trout) may act in a similar way by transporting nutrients from large rivers and lakes to higher elevation tributaries. However, the extent of nutrient transport is dwarfed by that of anadromous salmonids.

Status and potential for future changes:

Management of salmon populations is an active field of research and resource management at several levels of government. Populations of anadromous salmonids are affected by harvest of adults in coastal and inland fisheries, land and water use, pollution, climate change, and introductions of non-native species. Harvest rates vary through time and among stocks, but can exceed 50 percent for targeted stocks (e.g., Walters and Staley 1987). Harvest rates can be unsustainably high for endangered stocks that are harvested incidentally (e.g., Irvine 2002; COSEWIC 2003a, b). Land use impacts such as loss of riparian vegetation, drainage alterations, and pollution are additive and may produce a large incremental effect if combined with other activities (e.g., Bradford and Irvine 2000). Climate change is expected to have severe impacts

¹⁷ all species of salmon are semelparous – they reproduce and die shortly after. Rainbow, cutthroat and Dolly Varden are iteroparous, and therefore may return to the ocean after reproducing.

on fish distributions in BC through effects on precipitation (Morrison et al. 2002), streamflow (Leith and Whitfield 1998), water temperatures (BC Ministry of Environment 2006), and range changes in native and non-native species (e.g., Bonar et al. 2005; Fayram and Sibley 2000; Parmesan and Yohe 2003; Stefan et al. 2001; Welch et al. 1998).

Of 5,487 British Columbia anadromous salmonid stocks assessed by Slaney et al. (1996), 19.6% were deemed at risk (high risk, moderate risk or special concern) or extirpated. Although the remaining stocks were not below an at-risk threshold, it is likely that many are below historic abundance levels. Many of the at-risk stocks are relatively small stocks. Whereas abundance levels in systems with relatively large populations are likely adequate to maintain marine-derived nutrient inputs, many of the ecosystems with smaller stocks may be undergoing progressive oligotrophication due to declining nutrient inputs (Larkin and Slaney 1997). Some larger systems such as the upper Columbia River have lost all anadromous salmonids.

Relevance in BC:

This element is of widespread relevance in BC. Anadromous stocks are found throughout the Fraser River system and almost all coastal systems. Anadromous salmon were extirpated in the upper Columbia River due to impassable dams in the US. Historically anadromous stocks reached to Columbia Lake in the headwaters of the Columbia River. Anadromous stocks are absent in the Kootenay River systems due to natural barriers. They are also absent from the Peace River drainage, which drains east into the Mackenzie River system.

CONSEQUENCE OF CHANGE OR LOSS

Lower abundance or loss of this element would lead to lower abundance in many terrestrial and aquatic species and lower overall productivity of many bodies of freshwater (Wipfli et al. 1998, 2003).

MANAGEMENT FOR A HEALTHY ELEMENT

Anadromous salmon range over a broad geographic range and are therefore exposed to multiple threats. Management of this element therefore requires addressing these threats over the full geographic scale of these species. Management for a healthy element would include:

- sustainable harvest practices in coastal and inland fisheries
- sustainable land use practices with special attention to maintenance of riparian and floodplain habitats (to protect rearing and spawning habitats)
- sustainable water use with special attention to streamflow regulation (e.g., water diversions and dams)
- clean water (e.g., pollution control)
- incorporate predictions of climate change impacts in management tools and adjust management as necessary.

UNCERTAINTIES AND DATA GAPS

This is a well-studied group of organisms and most general patterns are well-known and based on studies with a high degree of confidence. There are many minor uncertainties, such as the strength of interactions with other components in the community, but these need not hinder implementation of sound management practices.

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2.11. KEY FRESHWATER SPECIES: KOKANEE

Kokanee is the common name used for the non-anadromous form of sockeye salmon (*Oncorhynchus nerka*). Kokanee spend their entire life cycle in freshwater and are often referred to as “landlocked.” In fact, they often co-occur with the anadromous form, in systems with access to the ocean. Molecular genetic evidence indicates that most kokanee populations have evolved independently rather than from a single event with subsequent range expansion. Kokanee and sockeye are able to cross-breed and offspring are viable, although mating between the two forms is not common. Kokanee are planktivorous; they rear in lakes and spawn in tributary streams or littoral areas with appropriate groundwater flow. Like sockeye, kokanee typically live four years and die shortly after spawning.

WHY IS THIS SPECIES IMPORTANT?

Functional Role:

Kokanee are an important component of many inland and coastal lake and river systems. Since all of their biomass is accumulated in situ, rather than during an ocean-rearing phase, kokanee generally have a much lower abundance and biomass than anadromous salmon. Yet they have similar functional roles in the ecosystems in which they are present due to their concentrated spawning period in tributary streams.

Kokanee act as a nutrient pump, bringing nutrients from lakes to nutrient poor tributaries (Richey et al. 1975). Somatic tissue accumulated as an obligate planktivore in lakes is transported to tributary systems when kokanee spawn. This temporal and spatial concentration of energy and nutrients creates an important food supply for many terrestrial and aquatic species. For example, eagles, bears, white sturgeon and other species cue on this abundant food source and it is thought that the abundance of these species depends critically on kokanee prey. Juvenile kokanee are a significant component of many freshwater communities and are an important food supply for birds and fish.

Functional Exclusivity:

Kokanee are not the sole species of salmonid inhabiting BC lakes or spawning in BC streams. However, in lakes where kokanee exist they often dominate abundance and biomass of fish species; other lake-dwelling salmonids are typically in lower abundance and have a smaller ecological role. To some extent other species with adfluvial forms like bull trout play a role in transporting nutrients to tributary systems from lower elevation lakes and rivers, but due to their numerical inferiority they play a less influential role in the ecosystem.

Status and potential for future changes:

Kokanee are most at-risk in southern British Columbia. They are well below historic abundance levels in the southern interior of British Columbia, in large part due to introduction of opossum shrimp (*Mysis relicta*) to many lakes in the Okanagan and Kootenay regions (e.g., Shepherd 2000). Shepherd (2000) noted that 1998 spawning populations of kokanee in Okanagan Lake were about 1% of 1970s levels. Most of this decline is attributed to the introduction of mysids, but water and land use are a significant contributing factor to habitat quantity and quality (Shepherd 2000; Northwest Hydraulic Consultants 2001). Populations are also affected by harvest, pollution, other non-native species and climate change.

Status in other parts of the province is not monitored as intensively although kokanee are an important species in many watersheds, especially some of the large hydro reservoirs.

Relevance in BC:

Kokanee are widespread in BC. The native distribution of kokanee includes all systems with ocean access, plus the upper Kootenay and Columbia systems. Stocking of kokanee in the

province has been fairly limited compared to other species and almost entirely within the native range of the species, with the exception of the east Kootenay watershed historically and the Peace-Williston reservoir more recently.

CONSEQUENCE OF CHANGE OR LOSS

The consequences of changes in kokanee abundance are reported in Spencer et al. (1991), who documented wide-ranging and cascading effects at multiple trophic levels following the introduction of mysids and the subsequent collapse of kokanee. They show a direct relationship between abundance of bald eagles and kokanee spawners. Unquantified observations indicated correlations in abundance with many bird species that feed on carcasses and eggs, and many terrestrial vertebrates such as coyote, mink and grizzly bears. Loss of this resource may not lead to extirpation of any of these species but it likely contributes to lower (potentially much lower) abundance of many aquatic and terrestrial species.

MANAGEMENT FOR A HEALTHY ELEMENT

Kokanee occur over a broad geographic range and are exposed to multiple threats. Management of this element therefore requires addressing these threats over the full geographic scale of these species. Management for a healthy element would include:

- prevent introductions of mysids and other non-native species
- support mitigation of effects of non-native species
- sustainable harvest practices of kokanee
- sustainable land use with special attention to maintenance of riparian and floodplain habitats (for spawning)
- sustainable water use with special attention to streamflow regulation (dams and water extraction)
- clean water (pollution)
- incorporate predictions of climate change impacts in management tools (adjust management as necessary)

UNCERTAINTIES AND DATA GAPS

Kokanee are generally well-studied, and most general patterns are well-known and based on studies with a high degree of confidence. There are many minor uncertainties, such as detailed population information for different kokanee stocks and the strength of relationships with other species in the community.

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2.12. KEY FRESHWATER HABITAT: RIVER FLOODPLAINS

Riparian zones are among the most productive and valuable of ecological systems. Besides forming a physical transition zone between aquatic and terrestrial ecosystems, there are often strong physical and biological interactions between the two. Ecological linkage, productivity and habitat complexity depends on an active floodplain, which is often absent or reduced due to agricultural, industrial and urban development, or from river regulation.

The terms riparian and floodplain are somewhat difficult to define precisely because they represent ecotones, or gradients between fully terrestrial and fully aquatic realms. We use the following definitions. The floodplain is that part of the river-floodplain ecosystem that is regularly flooded and dried, and it represents a type of wetland (Bayley 1995). Riparian areas include the floodplain and extend upslope to the immediately adjacent terraces (Naiman et al. 1998).

WHY IS THIS HABITAT IMPORTANT?

Functional Role:

Many aquatic species in BC are adapted to the seasonal flood dynamics that occur on river floodplains and make extensive use of these habitats. This can be seen in traits such as timing of certain life history events like spawning or hatch timing, and specific habitat requirements of certain life stages. For example, white sturgeon spawn on the ascending limb of the hydrograph which is thought to be in part an adaptation to allow juveniles use of seasonally-flooded floodplain habitats (Coutant 2004). Coho juveniles make extensive use of side and back channels, which are created and maintained by seasonal flood dynamics in the floodplain (Sandercock 1991).

The flood pulse is believed to enhance biological productivity and maintain diversity in the system through several mechanisms including increased habitat diversity and area, greater inputs of terrestrial material to the aquatic food web, decreased predation and competition, and high turnover of nutrients and organic matter (Junk et al. 1989; Corti et al. 1997; Winemiller and Jepsen 1998; Sommer et al. 2001).

Nutrients previously mineralized during the preceding dry phase are dissolved during the flooding phase. Additional nutrients dissolved in the flood waters or associated with suspended sediment are brought in from the main river. High primary production and decomposition rates also occur during flooding, with production exceeding decomposition (Bayley 1995). Fish production per unit area was found to be substantially greater in floodplain systems than in non-floodplain systems: flood pulses in large floodplains provide a bonus in production above what would be expected merely from the increase in water area (Bayley 1995; Sommer et al. 2001). Similar increases in invertebrate production have also been observed (Gladden and Smock 1990). An analysis has not been performed for species diversity, but given the biophysical complexity of floodplain habitats it seems likely that a similar "diversity bonus" would be found.

Functional Exclusivity:

Floodplain habitats are unique and there is minimal redundancy in this type of habitat. Different species depend on floodplain habitats to different extents. Dependence is usually a matter of degree and there are likely few or no aquatic vertebrates that have obligate needs

for this habitat. However, due to their high inherent productivity and habitat complexity, this is a habitat hot spot, with high abundance and high diversity for both aquatic and terrestrial species.

Status and potential for future changes:

The loss of floodplain habitats occurs from dyking, flow regulation, and modifications to the available floodplain. The loss and degradation of floodplain habitats has occurred historically, and continues to occur throughout BC, in watersheds of all sizes. The Fraser Basin downstream of Hope provides one example. Historically, significant flooding occurred annually along the lower Fraser during the spring freshet, which resulted in large tracts of swampy or marshy land (North and Teversham 1984; Perry 1984 cited in Boyle 1997). Sumas Lake varied in size from 32 to over 100 km² depending on water levels in the Fraser River (Schaepe 2001; Woods 2001), and was drained completely in 1920 for development of agricultural lands. The lake was shallow and marshy, and likely used by most fish species in the lower Fraser. Boyle et al. (1997) estimate that wetland area has declined from about 10% of the land area downstream of Hope to about 1%, with most changes occurring before 1930 (Boyle et al. 1997). Dyking in the Fraser Basin started as early as 1864; most of the approximately 600 km of existing dykes were constructed during the first half of the 20th Century (MWLAP 2002). Dredging and channelization have also occurred, and are ongoing (Lane and Rosenau 1995; RL&L 2000; Rosenau and Angelo 2000). This pattern or components of it have been repeated elsewhere in the province as streams are developed for hydropower and floodplains are claimed for agriculture and other development.

Overall, much of the low elevation floodplain habitat in BC has been converted to agricultural, industrial, housing or other use, particularly in the southern portion of the province and along major rivers. In many systems the great majority of floodplain is no longer accessible to wild populations of fish and wildlife (e.g., Boyle et al 1997). Much of the floodplain habitat in some systems (e.g., Columbia River) has been inundated by hydrodevelopment.

Relevance in BC: This habitat type is found throughout BC in virtually all biogeoclimatic zones. Due to the mountainous topography of BC the breadth of many riparian systems can be quite narrow, with broad floodplains restricted primarily to lower elevation medium and large river systems. Nevertheless, riparian and floodplain habitats have been repeatedly recognized as key habitats that deserve special management focus.

CONSEQUENCE OF CHANGE OR LOSS

Active floodplain can be considered a biodiversity habitat hot spot. Few vertebrate species in BC may have obligate needs for this habitat type, but its high inherent productivity and habitat complexity suggest that it is a significant habitat for many species. Loss or alteration of this habitat is likely to lead to decreased abundance of several terrestrial and aquatic vertebrate species.

MANAGEMENT FOR A HEALTHY ELEMENT

This habitat type occurs throughout BC and is exposed to multiple threats. Management for a healthy element would include:

- sustainable forest harvest practices in riparian and floodplain habitats
- sustainable land use practices with special attention to maintenance of riparian and floodplain habitats (for spawning)

- sustainable water use with special attention to streamflow regulation and maintenance of natural flow regimes (dams, water extraction and dyking)

UNCERTAINTIES AND DATA GAPS

The precise extent of floodplain habitat losses and alterations in BC are not known, but the general pattern is very clear as shown in the example above for the lower Fraser. The causal links between habitat changes and biodiversity losses are also not fully described, but this would be exceedingly difficult given the multidimensional nature of threats and changes to biodiversity in BC. Special studies are needed to examine specific hypotheses associated with the flood-pulse concept, but available data support the general hypothesis that a flood-pulse advantage increases biological productivity per unit water area above the level expected from equivalent stable-sized water bodies (Bayley 1995).

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2.13. KEY FRESHWATER HABITAT: LAKE – TRIBUTARY CONFLUENCES

Lake – tributary confluences occur in lakes at the confluence of inlet streams. These areas represent a gradient from stream to lake and are often important riparian and littoral habitats due to topography and inflowing nutrients and sediment.

WHY IS THIS HABITAT IMPORTANT?

Functional Role:

Lakes have longitudinal (i.e., horizontal) gradients in physical, chemical, and biological factors at points where tributaries enter. Kimmel and Groeger (1984) and Kimmel et al. (1990) divide this gradient into riverine, transition, and lacustrine zones. The extent and the properties of these zones depend greatly on the morphology of a lake and patterns of inflow. In particular, residence time and nutrient concentrations vary with basin morphology (Kennedy and Walker 1990). Deep, wide lakes dilute incoming nutrients more effectively than shallow, narrow waterbodies.

Inlet streams have sediment loads that penetrate into the lake and are primary sources of dissolved and particulate loads (Wetzel 1990). Inflow nutrient concentration usually declines along a gradient with distance from inlet confluence. The greatest loss of allochthonous nutrients occurs near the point of inflow, as particles suspended by turbulent stream flow settle out of the less turbulent lake water column. Sedimentation losses result initially from a decreased capacity for suspended particulates, but further downlake in the transition and lacustrine zones, nutrient concentrations decline due to uptake by phytoplankton and settling of organic matter (Kennedy and Walker 1990; Kimmel et al. 1990).

These processes point to lake – tributary confluences as high productivity hot spots within lakes. Indeed, this is often where highest density is found in a number of organisms. For example, white sturgeon are found in greatest abundance at lake – tributary confluences in Upper Arrow Lake and in Kootenay Lake (National Recovery Team for White Sturgeon 2006). The importance of nutrient inputs at lake – tributary confluences is underscored by other observations on Kootenay Lake: upstream impoundment on the Kootenay River coincided with a 25 – 50% decrease in biological productivity of Kootenay Lake (Kimmel et al. 1990).

Lake – tributary confluences provide high productivity habitats for a wide range of aquatic and terrestrial species.

Functional Exclusivity: Lake – tributary confluence habitats are unique and there is minimal redundancy in this type of habitat. Different species depend on these habitats to different extents. Dependence is usually a matter of degree and there are likely no aquatic vertebrates that have obligate needs for this habitat. However, due to their high inherent productivity and habitat complexity, this is a habitat hot spot, with high abundance and high diversity for both aquatic and terrestrial species.

Status and potential for future change:

There are no data available to directly assess the status of this key element.

However, lake – tributary confluences are affected by changes in inflow, outflow and water elevation, each of which are influenced by water use, land use and climate. Streamflow patterns in BC have changed in response to global climate change and this trend is expected to continue (Leith and Whitfield 1998; Morrison et al. 2002). Lake – tributary confluences are also influenced by land use impacts such as forest harvest where riparian systems are affected.

Relevance in BC: This element is of broad relevance in BC. Lakes with inlet streams are found throughout the province, and lake – tributary confluences are part of most of these systems. These habitats may be affected by altered flows in the inlet stream, water withdrawals from the lake, forest harvest in the watershed, and climate change. Many of these threats are projected to continue to increase as human population pressures increase in the province.

CONSEQUENCE OF CHANGE OR LOSS

Lake – tributary confluences represent an important habitat for many stream- and lake-dwelling organisms. These areas are key feeding and spawning areas, and their loss or alteration would negatively affect the abundance and distribution of many organisms that use this habitat.

MANAGEMENT FOR A HEALTHY ELEMENT

This habitat type occurs throughout BC and is exposed to multiple threats. Management for a healthy element would include:

- sustainable land use practices with special attention to maintenance of riparian and floodplain habitats (for spawning)
- sustainable water use with special attention to streamflow regulation and maintenance of natural flow regimes (dams, water extraction and dyking)
- incorporate predictions of climate change impacts in management tools and adjust management as necessary.

UNCERTAINTIES AND DATA GAPS

This type of habitat is not typically monitored effectively, so the extent of lake – tributary confluence habitat losses and alterations in BC are not known. The causal links between habitat changes and biodiversity losses are also not fully described, but this would be difficult given the multidimensional nature of threats and changes to biodiversity in BC.

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2.14. KEY FRESHWATER HABITAT: ESTUARIES

An estuary is "a semi-enclosed coastal body of water which has a free connection with the open sea and within which sea water is measurably diluted by fresh water from land drainage" (Pritchard 1967). Estuaries are generally believed to be unusually productive in comparison to other aquatic systems, and even in comparison to cultivated lands (Correll 1978; Beck et al. 2001). They also have a critical role as spawning and nursery grounds for many species of fish and invertebrates, and function as critical feeding and resting areas for many species of water birds. For example, the Fraser River estuary is a nursery to all species of eastern Pacific salmon, and is known to play a substantial role in making the Fraser the largest salmon-producing river in North America. Likewise, migratory birds are highly dependent on this habitat for food and protection during long-range migrations (Flynn et al. 2006).

Estuaries are a form of ecotone, a gradient from freshwater to marine, and as a result offer diverse habitats and food sources and often support abundant flora and fauna. High species abundance results from high levels of in situ biological production, and also the high degree of spatial complexity that affords protection from predators (Boesch and Turner 1984). Because the marine environment is tidal, there are also temporal and spatial elements to estuaries, which include intertidal and subtidal regions. Estuarine ecology is complex because of the interaction between freshwater, marine and terrestrial elements. Water in estuaries is brackish, or a mixture of freshwater and saltwater, and organisms that live here must generally have wider tolerances in salinity than obligate freshwater or marine fauna. Estuaries are productive because of the constant inputs of sediment and nutrients from freshwater systems, but they are also efficient at recycling and retaining nutrients.

Estuarine ecosystems provide substantial and valuable ecological services. Most of the largest cities on the planet are built on estuaries. Much of the world's fisheries and aquaculture production is dependent on estuaries (Houde and Rutherford 1993). Estuaries are important filters of pollutants such as herbicides, pesticides, and heavy metals out of the water, as well as excess sediments and nutrients (USEPA 2006). Estuaries are also buffer zones that stabilize shorelines and protect coastal areas, inland habitats and human communities from floods and storm surges.

WHY IS THIS HABITAT IMPORTANT?

Functional Role:

Estuaries have high intrinsic productivity and also provide key refuge habitat for critical life stages of many fish and invertebrates. This productivity is also heavily exploited by terrestrial species. Estuaries play a substantial role in the life history of many commercially important fish species (e.g., salmon, herring, eulachon), and species such as migratory birds are highly dependent on this habitat for food and protection during long-range migrations.

Functional Exclusivity:

There is minimal redundancy in this type of habitat, as there are no other coastal habitats with similar features. Different species depend on these habitats to different extents, but estuaries are often thought of as both a diversity and abundance hotspot. For example, migratory birds are highly dependent on this habitat for food and protection during long range migrations (Flynn et al. 2006). The Fraser River estuary is a nursery to all species of salmon, and is known to play a substantial role in making the Fraser the largest salmon-producing river in North America. Due to their high inherent productivity and habitat complexity, this is a habitat hot spot, with high abundance and high diversity for both aquatic and terrestrial species.

Status and potential for future changes:

Coastal cities and towns occur at many of the major estuaries in BC (e.g., Vancouver, Nanaimo, Prince Rupert), and direct and indirect impacts are many. Estuaries are affected by changes in inflow, sedimentation, dredging, and land use. Streamflow patterns are affected by river regulation, water use and global climate change (Poff et al. 1997; Leith and Whitfield 1998; Morrison et al. 2002). Sediment transport is affected by river regulation, dams, dredging, instream and floodplain gravel mining, and inputs from land use changes (Baxter 1977; Ligon et al. 1995). Dredging can influence flow patterns and sediment deposition, and alter quality and quantity of aquatic habitats. Land use can alter habitat availability, particularly through dyking and land reclamation practices (Boyle et al. 1997). Land use can also alter the rate at which sediments are mobilized and transported to streams (Hartman et al. 1996). For example, approximately 70% of the Fraser River estuary wetlands have been diked, drained and filled. Similar statistics exist for major estuaries on Vancouver Island such as Nanaimo and Cowichan estuaries (Flynn et al. 2006).

Relevance in BC: Estuaries are of broad relevance to biodiversity in BC. Estuaries of many sizes occur over the long and varied coastline of the province, from the Fraser River estuary to the many small coastal streams in BC. Many estuaries are directly and indirectly impacted by coastal cities and towns that are built on portions of major estuaries, and by other impacts occurring in the watershed. Estuarine habitats are threatened by many activities, and the threats are likely to continue as human population pressures increase in the province. At the same time the ecosystem services provided by estuaries, ensures their relevance to the human economic system.

CONSEQUENCE OF CHANGE OR LOSS

As noted above, estuaries provide important ecosystem services and direct economic benefits. Many coastal fisheries are dependent on healthy ecosystems. Likewise, many species are dependent on estuaries at some point in their life history. Estuaries are key feeding and spawning areas, and their loss or alteration would negatively affect the abundance and distribution of many organisms that use this habitat.

MANAGEMENT FOR A HEALTHY ELEMENT

This habitat type occurs throughout coastal BC and is exposed to multiple threats. Management for a healthy element would include:

- limitation of destruction or alteration of foreshore habitats in estuaries
- sustainable land use practices with special attention to retention of processes to ensure natural sediment dynamics
- sustainable water use practices with special attention to streamflow regulation and maintenance of natural flow regimes (dams, water extraction and dyking)
- minimize pollutant discharges that can build up in estuarine sediments or affect productivity of estuarine organisms.

UNCERTAINTIES AND DATA GAPS

This type of habitat is not typically monitored continuously and effectively across the province, so the extent and trends of estuarine habitat losses and alterations in BC are not known. The causal links between habitat changes and biodiversity losses are also not fully described, but this would be difficult given the multidimensional nature of threats and changes to biodiversity in BC.

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2.15. KEY FRESHWATER PROCESS: RIVER FLOW REGIME

The flow regime of a river is the temporal pattern of surface flows in a specific stream at a specific location. Stream flows are affected by several aspects of climate (e.g., precipitation, temperature, solar radiation, evapotranspiration) and the physical setting (e.g., geology, streambed material, channel shape, gradient). BC is hydrologically diverse and the natural flow regime varies considerably among geographic regions of the province.

Humans have altered the flow regime in numerous BC streams through dams, water diversions and extractions, land use changes, dredging and dykes. Altered flow regimes affect the quantity and quality of instream and riparian habitats, and the abundance and distribution of aquatic and riparian organisms. Several physical and chemical properties of water, such as temperature, nutrients, and dissolved oxygen, may be affected by altered flow regimes. Climate change is already having noticeable effects on streamflow patterns in some areas of BC.

WHY IS THIS PROCESS IMPORTANT?

Functional Role:

It is somewhat of a truism that native species are adapted to the natural flow regime, since these are the conditions under which they have evolved (Lytle and Poff 2004). Some aspects of flow regime, such as floods and drought, are best described as disturbances and native species often have specific life history adaptations to these disturbances. For example, in an examination of rainbow trout introductions worldwide, Fausch et al. (2001) found that successful invasion was best predicted by a match between the hydrologic timing of flooding and emergence time of fry. Introductions were most successful when receiving habitats had disturbance regimes (e.g., timing and magnitude of flood events) similar to those within the species' native range. Delucchi (1988) found that benthic invertebrate community structure in small streams was related to temporal flow regime, and many benthic fauna species have general adaptations, such as high migration rates, drought-resistant eggs, and the tendency to take refuge in the hyporheic zone. Cottonwood, a key riparian plant in BC, has seed maturation timing that is an adaptation to timing of snowmelt floods, and when flood timing changes significant mortality results (Mahoney and Rood 1998).

Flow regime has many effects on instream habitat. Stream habitat tends to be classified at three scales: the watershed- or reach-level "macro" scale (e.g., elevation, gradient, channel width, etc.), the stream segment-level "meso" scale (e.g., riffle, run, pool, etc.), and the hydraulic -level or "micro" scale (e.g., depth, velocity, substrate, etc.). When defining and quantifying habitats in a stream, there is a greater dependence on flow at the micro scale than at the macro scale. For example, elevation and stream gradient are insensitive to flow except over geological time scales. Mesohabitats are affected by changes to flow because habitat boundaries and habitat types shift with changes in flow; at low flows a particular site may be a pool, while at higher flows it may be a riffle (Heger et al. 1996; Hilderbrand et al. 1999; Parasiewicz 2001), but they change little over small to moderate flow increments. Distribution and abundance of microhabitats are especially sensitive to changes in flow since depths and velocities at any particular site will change with flow, sometimes quite substantially over relatively small flow changes. Abundance and distribution of fish and other organism is directly related to many of these habitat variables (e.g., Rosenfeld et al. 2000; Sharma and Hilborn 2001; Beecher et al. 1993, 1995; Bradford et al. 1997, 2000).

There have been many significant changes in habitat and biological components as a result of changes to flow regime. For example, on the Trinity River in northern California river managers implemented a single release of $4.2 \text{ m}^3 \text{ s}^{-1}$ from Lewiston Dam, believing this would maximize spawning habitat for chinook salmon. The chain of events that followed resulted in a narrow, armoured channel, cut off from the floodplain, with disastrous effects for fish and a variety of other species (Trush et al. 2000). In BC, on the Big Qualicum River a dam was constructed specifically to regulate flows to enhance fish production. Although there was an initial positive biotic response to changes in the flow regime, longer term trends were decidedly negative as the streambed became infiltrated with fines (Lewis and Mitchell 1994). In short, flow regime has an enormous effect on habitat availability and complexity, and changes to flow regime have many direct and indirect effects on biological components of instream communities.

Functional Exclusivity:

Flow regime has been described as a “master variable” (Poff et al. 1997) that controls a suite of physical variables that in turn influence biological production through a number of direct and indirect pathways. In some instances it is possible to address some of these aspects directly rather than through flow. For example, streambed sediment quality can be addressed through management of short term pulses or “flushing flows,” riparian qualities can be manipulated through selective planting and harvest techniques, water temperatures can be mitigated through manipulation of surface and hypolimnetic releases. However, in most cases such solutions are partial or temporary and other issues may not be resolvable through engineering approaches. Strategies using the “natural flow regime” try to quantitatively describe and then preserve key aspects of the natural hydrograph (Poff et al. 1997; Richter et al. 1996, 1997; Trush et al. 2000).

Status and potential for future changes:

Numerous rivers in BC are regulated for hydropower and flood control, including major rivers such as the Columbia, Kootenay and Peace Rivers. Many moderate size rivers have also been developed for hydropower, and the province is currently undergoing rapid expansion of hydropower development on smaller size streams.

Changes in flow are capable of affecting instream and riparian biota, with the magnitude of change in biota generally being proportional to changes in flow. Potential changes include altered riparian communities (e.g., Johnson 1994, 1995), altered invertebrate communities (e.g., Spence and Hynes 1971; Zhang et al. 1998; Morgan et al. 1991), and altered fish communities (e.g., Wolff et al. 1990; Smith 2000; Marchetti and Moyle 2001; Harvey et al. 2006). Streamflow patterns in BC have changed in response to global climate change and this trend is expected to continue (Leith and Whitfield 1998; Morrison et al. 2002). These changes are expected to influence ranges of native and non-native species.

Relevance in BC:

This key element is of broad relevance in BC. Regulated streams are found throughout the province, as are those with flows affected by water withdrawals, forest harvest, and climate change. Hydropower projects have been proposed for many other streams, and water use is projected to continue to increase as human population pressures increase in the region. Climate change has already affected patterns of surface flow in some regions, and will continue to modify flow regime.

CONSEQUENCE OF CHANGE OR LOSS

Flow regime is proposed as a key element because it has direct and indirect influences on aquatic and riparian habitat quantity and quality. Evidence clearly demonstrates that changes to the natural flow regime often have negative consequences for native biodiversity through lower abundance of native species, increased abundance of non-native species, and extirpation of native species. The magnitude of effect is related to the magnitude of flow alteration.

MANAGEMENT FOR A HEALTHY ELEMENT

This process is relevant throughout BC and is affected by many human uses of land and water. Management for a healthy element would include:

- sustainable land use practices with special attention to maintenance of riparian and floodplain habitats and practices that may alter runoff patterns
- sustainable water use practices with special attention to streamflow regulation and maintenance of natural flow regimes (dams, water extraction and dyking)
- incorporate predictions of climate change impacts in management tools and adjust management as necessary.

UNCERTAINTIES AND DATA GAPS

The general linkages between flow regime and channel morphology, habitat quantity and quality, and many species responses are well understood and supported by abundant scientific literature. Despite good support for general patterns there is considerable variation in responses to altered flow regimes, and the magnitude of response is usually related to the magnitude of flow change. It remains difficult to predict in detail the longterm physical and biological outcomes of changes to flow regimes (Castleberry et al. 1996).

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2.16. KEY FRESHWATER PROCESS: LAKE LEVELS

As a key element, lake levels refer to the temporal pattern of water elevations in a specific lake. Lake levels are affected by several aspects of climate (e.g., precipitation, temperature, solar radiation, evapotranspiration) and the physical setting (e.g., geology, basin shape, basin size). BC is hydrologically and biogeoclimatically diverse and natural lake level patterns vary considerably among geographic regions of the province.

Humans affect lake levels through dams, water diversions and extractions, and land use changes. Altered lake levels affect the quantity and quality of littoral and riparian habitats, and the abundance and distribution of aquatic and riparian organisms. Several physical and chemical properties of water, such as temperature, nutrients, and dissolved oxygen, may be directly or indirectly affected by lake levels. Climate change is already having noticeable effects on streamflow patterns in some areas of BC, which will likely affect lake levels.

WHY IS THIS PROCESS IMPORTANT?

Functional Role:

Emergent and submerged aquatic macrophytes are the dominant structural component of littoral habitats. They provide food and shelter for a wide variety of invertebrates, fish and wildlife. Vegetation responds to the strong gradient between the terrestrial and aquatic interface and under most natural conditions there is strong zonation of vegetation along this gradient. Keddy and Resnicek (1986) distinguish among four main zones: forest and shrub thicket, wet meadow, marsh and aquatic. Wet meadow and marsh are found solely within the zone affected by fluctuating water levels.

Fluctuating water levels are considered the most important factor determining vegetation patterns on lake shores, although other factors such as wave exposure, soil or sediment type, and species interactions are also influential. The effect of water level and drawdown on macrophyte distribution and abundance has been fairly well studied, though results have been variable due to differences among studies in lake geology, morphometry, species affected, and differences in drawdown scenarios (Turner et al. 2005).

The photic zone, the depth strata where plants can live, does not extend to the deepest portions of a lake because light intensity is attenuated as it travels through water. As a lake is drawn down wetted areas are exposed and the photic zone shifts to deeper elevations in the lake basin. The frequency, duration and magnitude of the drawdown determines the effect on vegetation.

Under most normal conditions water level fluctuations occur due to seasonal changes in the water budget. Fluctuations give rise to distinct zonation patterns in littoral vegetation, as different species are adapted and tolerant to different water levels. As water level fluctuations increase in magnitude (e.g., due to water management) vegetation responds and often there is a decrease in the effective littoral zone. The effective littoral zone decreases because high elevation areas are inundated insufficiently to support emergent species, and inundated too frequently to support upland vegetation. Low elevation areas are unproductive because the photic zone extends to these areas for insufficient time to allow establishment of submerged macrophytes. This general model is useful for understanding the effects of water level fluctuations on vegetation patterns in lakes and reservoirs, and related effects on riparian and aquatic animals.

Rorslett (1989) found that fluctuations of 5 to 7 m completely removed macrophytes from the littoral zone in oligotrophic lakes in Scotland and Norway, which is consistent with results of

other studies (e.g., Hellsten et al. 1996; Paller 1997; Turner et al. 2005). Sooke Reservoir with a drawdown of over 6 m has almost no macrophytes (Furey et al. 2004). The general trend is that as the amplitude of fluctuations increases, the width of littoral vegetation decreases (Turner et al. 2005). Relatively minor shifts in average annual water levels (± 10 cm) or in water level fluctuations can produce substantial changes in the vegetation community (Magee and Kentula 2005). Species changes are common, even after a single drawdown (Turner et al. 2005). The magnitude of fluctuations is one of the primary differences between reservoirs and natural lakes, and causes extirpation of littoral and shoreline vegetation from most hydropower reservoirs (Wetzel 1990). Stabilized water levels are also capable of significant effects on littoral macrophyte diversity (Wilcox and Meeker 1991). There have been fewer studies of submerged macrophyte response to drawdown. Turner et al. (2005) noted that the response of submerged macrophytes to drawdown was species-specific. Some species were very sensitive to the drawdown, while others were capable of fast vegetative growth or germination from seeds or other propagules. In general, however, there was a decrease in species richness, cover and biomass of submerged macrophytes.

Several other ecologically important effects from drawdowns deserve brief mention. In an early review, Cooke (1980) suggested that drawdowns, particularly severe drawdowns, would lead to algal blooms through release of nutrients from exposed littoral areas and subsequent limited uptake of nutrients in littoral habitats. Some researchers (e.g., Turner et al. 2005) have not observed this effect, though it is considered a valid possibility and has occurred in some studies (e.g., James et al. 2001). Other studies have noted considerable consolidation and compaction of exposed littoral sediments (e.g., Kadlec 1962) and some have noted desiccation and erosion of exposed soils (Turner et al. 2005). Indeed repeated drawdowns are the primary cause of coarse sediments dominating exposed littoral areas of hydropower reservoirs. Littoral invertebrate populations can be severely reduced by drawdown (Kadlec 1962) and many studies have shown correlations between fish abundance and diversity and water levels (e.g., Cohen and Radomski 1993; Paller 1997).

Functional Exclusivity:

Lake levels are related to a suite of physical variables that in turn influence biological production through a number of direct and indirect pathways. In some instances it is possible to address habitat issues through engineering solutions such as selective riparian planting and harvest techniques, nutrient enrichments or wildlife enhancements. However, in most cases such approaches offer only partial or temporary mitigation and other issues may not be resolvable through engineering approaches.

Status and potential for future changes:

Hydropower development is widespread in BC, and inundation of natural lakes or formation of large reservoirs has played a significant role in many of these projects. Flood control projects also regulate water levels in many lakes (e.g., Okanagan and Columbia Rivers). Alteration of lake levels tends to be associated with larger hydropower and flood control projects and few such projects have been built in recent years. Nevertheless, many such projects exist in BC. Lake levels may also be affected by drawdowns associated with licensed water extractions. The extent of these impacts is not known, but may increase in response to climate changes.

Patterns in lake levels can be described with several parameters:

- Magnitude: the difference in water level elevations between two time periods. Biological impacts are expected to be proportional to lake level changes.

- Frequency: the number of events of a given magnitude per time interval (e.g., per year). Frequency is typically related inversely to magnitude, since events of large magnitude are rare.
- Duration: the period of time associated with a particular lake level.
- Timing: the date during the year that an event (e.g., flood or drought) occurs.
- Predictability: the degree to which flood or drought events are autocorrelated temporally, typically on an annual cycle. Predictable events might also be correlated with other environmental signals (e.g. rainfall events, seasonal thermal extremes, sudden increases or decreases in flow).

Water use, land use and climate change affect each of these parameters.

Relevance in BC:

This key element is of broad relevance in BC. Water licenses affecting lake levels exist throughout the province, and other activities affecting hydrologic processes and ultimately lake levels are also widespread, including forest harvest, other land uses, and climate change. Climate change has already affected patterns of surface flow in some regions, and will continue to modify flow regimes and lake levels.

CONSEQUENCE OF CHANGE OR LOSS

When effective littoral area declines with increased water level fluctuations, littoral primary and secondary production is lost from the system. Therefore, in lacustrine environments with large water level fluctuations pelagic production becomes a more dominant energy source, with concomitant effects on invertebrates, fish and other wildlife. Several studies have shown strong coupling between benthic and pelagic production when littoral areas are relatively undisturbed (e.g., Hecky and Hesslein 1995). Linkages between terrestrial and aquatic environments may be lost, with lower riparian production and potential loss of wildlife habitats. In some cases, lower lake levels can reduce or extinguish outflows and thus extirpate productive aquatic and riparian habitats.

MANAGEMENT FOR A HEALTHY ELEMENT

Lakes occur throughout BC and are exposed to multiple water and land uses. Management for a healthy element would include:

- sustainable land use practices with special attention to maintenance of riparian and floodplain habitats (for spawning)
- sustainable water use with special attention to streamflow regulation and maintenance of natural flow regimes (dams, water extraction and dyking)
- incorporate predictions of climate change impacts in management tools and adjust management as necessary

UNCERTAINTIES AND DATA GAPS

The link between lake levels and biological effects is most well-studied for reservoir systems around the world. This literature is well-developed and offers many insights into the relationship between lake levels and various aspects of riparian and reservoir biology. The literature is less well-developed for effects of smaller lake level changes, but even here the general trends are well-known and supported by scientific data. Nevertheless, it remains difficult to predict in detail the longterm physical and biological outcomes of changes in lake level due to differences in physical and ecological settings.

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2.17. KEY FRESHWATER PROCESS: GROUNDWATER-SURFACE WATER INTERACTIONS

Freshwater ecologists have started to consider interactions between surface water and groundwater only fairly recently (Hynes 1983). The study of groundwater has more traditionally been the domain of hydrologists, whereas ecologists have largely been interested in ecological interactions within surface waters. There has been a flurry of ecological research interest in groundwater and the hyporheic zone, the saturated sediment zone that is a transitional gradient between surface water and deeper groundwater. This interest has been spurred in part by studies such as that of Stanford and Ward (1988) who found a rich flora of riverine invertebrates in shallow (10 m) wells located on the flood-plain up to 2 km from the channel of the Flathead River, Montana. At the same time there has been a growing appreciation of the chemical and physical interactions between surface water and groundwater, as mediated in large part by the rich invertebrate biota dwelling in the hyporheic zone and the temperature differences between surface and groundwater (Edwards 1998).

There has also been great interest in groundwater upwelling and its effect on the habitat use of stream fishes. For example, many fish have been shown to key on groundwater sources at different times of year. Baxter and McPhail (1999) observed that bull trout made extensive use of groundwater upwelling sites for spawning, and found that incubation was considerably more successful there than in adjacent non-upwelling sites. Similar results have been reported for other spawning salmonids in lakes, streams and reservoirs (Lorenz and Eiler 1989; Lemay 1993; Curry et al. 1994; Garrett et al. 1998). Migrating chinook adults have been observed to take advantage of cool groundwater upwelling sites for holding, at times when many nearby stream locations were beyond the physiological thermal limits for the species (Torgersen et al. 1999; Geist 2000). Groundwater release can be important in winter too, as upwelling areas are often warmer and prevent freezing of spawning and rearing areas (Baxter and McPhail 1999; Bradford et al. 2001).

As knowledge of the ecological values of groundwater resources has accumulated, so too has an appreciation of how human activities influence groundwater-surface water interactions and the concomitant effects on biodiversity values (e.g., Stanford and Ward 1993; Boulton et al 1997; Brunke and Gonser 1997; Sophocleous 2000; Allen et al 2004).

WHY IS THIS PROCESS IMPORTANT?

Functional Role: Surface waters are the most readily apparent component of the hydrologic cycle, but in most areas of BC there is a strong interaction between surface flows and groundwater resources. This is perhaps intuitive since surface flows in perennial streams continue long after precipitation or snowmelt runoff events. Groundwater is recharged by infiltration from precipitation and surface flow, and depending on the depth of the water table and subsurface geology groundwater may be subsequently released as surface flow (Sophocleous 2002). This release to surface water forms most of the base flow for many streams through periods of no precipitation, or during winter when precipitation is locked up as snow or ice (Sophocleous 2002). This base flow is of extreme importance to organisms such as fish, as it is often changes in base flow that have direct effects on fish fauna (e.g., Harvey et al. 2006). In winter, this base flow release is typically warmer than ambient surface water and may prevent freezing conditions in spawning and rearing areas (Baxter and McPhail 1999; Bradford et al. 2001). In summer, groundwater is often cooler than ambient, which can help keep stream temperatures within thermal tolerance limits of native fish species (Torgersen et al. 1999). This base flow also keeps the stream wetted and flowing between periods of precipitation, and can be critical to survival of fish (Bradford et al. 1997; Harvey et al. 2006). The hyporheic zone is thought to be a critical refuge for surface-dwelling invertebrates, and most insect families and other groups that live in surface waters have been collected from the hyporheic zone (Boulton et al 1998). Nutrients released to surface waters from the hyporheic zone are also known to influence surface water quality and productivity, to the point of creating productivity hotspots in some instances (Boulton et al 1998; Edwards 1998).

Functional Exclusivity: Groundwater typically represents an enormous storage volume of cool, clean water. This natural storage source is unique and there is no redundancy in this source beyond its large volume. It may be possible to offset groundwater losses with surface storage, but this would typically be expensive and infeasible at large scales. Given the usual temperature and chemical differences between surface and groundwater, large scale surface storage would also be a poor replacement of groundwater.

Status and potential for future changes: Groundwater and surface water can be influenced directly by a number of factors, including climate, land use, water use, and industrial activities. How each of these act within a particular watershed is rarely straightforward but there are

many examples linking human activities to changes in quality and quantity of groundwater and surface water, and interactions between the two water sources. Some examples include the following:

- when groundwater is abstracted for human use there can be direct, measurable influences on base flow in streams (Sophocleous 2000, 2002)
- changes to water table levels can significantly influence riparian vegetation (Stanford and Ward 1993)
- changes to streambed embeddedness (e.g., through river regulation, sediment inputs, eutrophication) has a direct impact on water table levels by altering infiltration and exfiltration rates (Brunke and Gonser 1997)
- release of toxic and organic pollutants into surface waters can infiltrate and alter groundwater quality (Brunke and Gonser 1997)
- altering land cover from forest to pasture has effects on hyporheic temperatures (Boulton et al 1997)
- groundwater recharge rates are closely linked to climate and precipitation, which are expected to be modified under climate change scenarios (Allen et al 2004; Scibek 2005)
- in urban areas, changes to impervious surfaces can have a large influence on runoff and groundwater recharge, with concomitant effects to base flows and peak flows in streams (Booth et al. 2002; Wang et al 2002)
- and agricultural settings, changes in land cover, drainage and irrigation can have severe impact on streamflows (Boulton et al 1997; Sophocleous 2000; Pearson et al. 2006).

Overall, Groundwater resources are of considerable concern in a number of locales in BC, particularly in the southern portion of the province where agricultural, municipal and industrial demands for groundwater are highest. Approximately 25% of BC residents obtain drinking water from groundwater sources and government regulation and monitoring of this resource has increased in recent years (Smerdon and Redding 2007). 35 aquifers were designated as “heavily-used” in 2001, up from 17 in 1996 (MWLAP 2002). 139 wells have been regularly monitored for water levels (MWLAP 2002). Monitoring data indicate that groundwater levels are declining in areas where groundwater withdrawal and urban development are most intensive (MWLAP 2002).

Relevance in BC:

This key element is of broad relevance in BC. Water licenses control access to surface water abstraction, whereas there is typically less regulatory control of groundwater abstraction, and only rarely is groundwater use controlled for the purpose of limiting ecological impacts. Groundwater-surface water interactions occur in all watersheds in BC, and will be affected by many human activities, including land use (e.g., urbanization, forest harvest, agriculture practices), water use (e.g., hydropower development, river regulation, surface water and groundwater abstraction), and indirect effects (e.g., climate change).

CONSEQUENCE OF CHANGE OR LOSS

Changes to groundwater resources will have varying impacts to biodiversity depending greatly on the physical and ecological setting. Some species, such as the diverse hyporheic community, are directly dependent on groundwater resources. Other species and

communities are less obligately dependent, but large and measurable consequences are nevertheless likely. For example, many species of fish use groundwater upwelling areas as spawning habitat or holding habitats during migrations. Loss of these features is expected to cause lower incubation success and higher levels of physiological stress, both potentially causing lower abundance of adult and juvenile fish and replacement by more tolerant species. Lower water tables can have profound effects on riparian and floodplain vegetation, with cascading effects on local biodiversity and physical effects such as lower streambank stability.

MANAGEMENT FOR A HEALTHY ELEMENT

Management of groundwater resources for biodiversity values must start with acknowledging the potential for groundwater-surface water dynamics (Edwards 1998) and planning within a risk-averse decision framework. For example, base flow conditions are often thought to limit fish production in streams (Harvey et al. 2006), and human activities that affect base flows can directly influence fish abundance and distribution. At present, there is typically greater regulatory control of surface water abstraction than groundwater abstraction, and only rarely is groundwater use controlled for the purpose of limiting ecological impacts. Often the use of groundwater is poorly monitored, such that the cumulative use of groundwater resources is not well known in many watersheds. In many cases the causal links between groundwater and surface water are based on general theory rather than specific knowledge of subsurface geology and groundwater dynamics.

UNCERTAINTIES AND DATA GAPS

Within a watershed there are large uncertainties in where groundwater is, how it moves, locations and rates of groundwater – surface water exchange, aquifer recharge rates, and impacts of land use, water use and climate change. Filling these data gaps is not a trivial task and requires detailed knowledge of subsurface geology, seasonal and long-term groundwater dynamics, and ecological dependencies. Within BC, work is underway on hydrologic modeling and measurement of some high value aquifers, and stream and lake ecologists are starting to incorporate knowledge of groundwater dynamics into their studies. Yet, there remains a great deal to learn before this resource can be knowledgeably managed.

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APPENDIX 1: SUMMARY OF THE NUMBER OF KEY ECOLOGICAL FUNCTIONS PLAYED BY VERTEBRATE SPECIES IN THE COLUMBIA BASIN.

From Pandion 2001.

Common Name	Total	Blue-winged Teal	17
Black Bear	32	Bonaparte's Gull	17
Raccoon	27	Cascade Golden-mantled Ground Squirrel	17
Deer Mouse	26	Cassin's Finch	17
Beaver	24	Fisher	17
Golden-mantled Ground Squirrel	24	Franklin's Gull	17
Woodchuck	24	Great Blue Heron	17
American Coot	23	House Finch	17
Douglas' Squirrel	23	Mink	17
Red Squirrel	23	Muskrat	17
Grizzly Bear	22	Pine Siskin	17
Sandhill Crane	22	Ring-necked Duck	17
Striped Skunk	22	Sharp-tailed Grouse	17
American Crow	21	White-crowned Sparrow	17
Mallard	21	Wild Turkey	17
Black-billed Magpie	20	American Goldfinch	16
Common Raven	20	Black-capped Chickadee	16
Elk	20	Black-headed Grosbeak	16
Herring Gull	20	Bushy-tailed Woodrat	16
House Mouse	20	Canada Goose	16
Ring-billed Gull	20	Columbian Ground Squirrel	16
Snowshoe Hare	20	Common Goldeneye	16
American Wigeon	19	Glaucous-winged Gull	16
California Gull	19	Gray Jay	16
Canvasback	19	Gray Wolf	16
Gadwall	19	Hoary Marmot	16
Glaucous Gull	19	House Sparrow	16
Redhead	19	Lesser Scaup	16
Rusty Blackbird	19	Meadow Vole	16
Townsend's Chipmunk	19	Mew Gull	16
Cinnamon Teal	18	Northern Flying Squirrel	16
Common Merganser	18	Northern Shoveler	16
Coyote	18	Purple Finch	16
European Starling	18	Red-tailed Chipmunk	16
Greater White-fronted Goose	18	Ring-necked Pheasant	16
Green-winged Teal	18	Ruffed Grouse	16
Hooded Merganser	18	Sora	16
Keen's Mouse	18	Steller's Jay	16
Least Chipmunk	18	Western Grebe	16
Mule Deer	18	Western Harvest Mouse	16
Northern Pintail	18	Wilson's Phalarope	16
Snow Goose	18	Wood Duck	16
Trumpeter Swan	18	Belted Kingfisher	15
Yellow-pine Chipmunk	18	Bohemian Waxwing	15
Black Tern	17		
Black-crowned Night-heron	17		

Bullock's Oriole	15	Lazuli Bunting	14
Caspian Tern	15	Mountain Chickadee	14
Chipping Sparrow	15	Pacific Chorus Frog	14
Eastern Fox Squirrel	15	Pine Grosbeak	14
Evening Grosbeak	15	Red-breasted Merganser	14
Forster's Tern	15	Ruddy Duck	14
Fox Sparrow	15	Shrew-mole	14
Great Basin Spadefoot	15	Spotted Sandpiper	14
Lincoln's Sparrow	15	Virginia Rail	14
Long-billed Curlew	15	Western Kingbird	14
Long-toed Salamander	15	Western Terrestrial Garter Snake	14
Mountain Beaver	15	White-breasted Nuthatch	14
Nuttall's (Mountain) Cottontail	15	White-tailed Deer	14
Porcupine	15	White-tailed Ptarmigan	14
Red-breasted Nuthatch	15	Yellow-bellied Marmot	14
Red-necked Phalarope	15	Barrow's Goldeneye	13
Sage Thrasher	15	Blue Jay	13
Savannah Sparrow	15	Brewer's Blackbird	13
Snow Bunting	15	Caribou	13
Song Sparrow	15	Cassin's Vireo	13
Tiger Salamander	15	Common Pika	13
Varied Thrush	15	Dark-eyed Junco	13
Vesper Sparrow	15	Eared Grebe	13
Western Toad	15	Great Basin Pocket Mouse	13
White-tailed Jackrabbit	15	Harris's Sparrow	13
Williamson's Sapsucker	15	Horned Grebe	13
Wood Frog	15	Killdeer	13
American Avocet	14	Least Flycatcher	13
American Marten	14	Magnolia Warbler	13
American Tree Sparrow	14	Montane Vole	13
Bald Eagle	14	Nashville Warbler	13
Barred Owl	14	Northern Leopard Frog	13
Blue Grouse	14	Northern Pocket Gopher	13
Brewer's Sparrow	14	Pacific Jumping Mouse	13
Bufflehead	14	Pacific-slope Flycatcher	13
Bullfrog	14	Red Crossbill	13
California Quail	14	Red-naped Sapsucker	13
Cedar Waxwing	14	Red-necked Grebe	13
Chestnut-backed Chickadee	14	Ruby-crowned Kinglet	13
Chukar	14	Southern Red-backed Vole	13
Clark's Nutcracker	14	Spotted Towhee	13
Clay-colored Sparrow	14	Swainson's Thrush	13
Common Redpoll	14	Tennessee Warbler	13
Common Tern	14	Tundra Swan	13
Eastern Kingbird	14	Veery	13
Golden-crowned Sparrow	14	White-throated Sparrow	13
Grasshopper Sparrow	14	American Badger	12
Gray Catbird	14	American Robin	12
Gray Partridge	14	Boreal Chickadee	12
Lark Sparrow	14		

Brown-headed Cowbird	12	Sharp-shinned Hawk	11
Burrowing Owl	12	Silver-haired Bat	11
Columbia Spotted Frog	12	Tree Swallow	11
Common Garter Snake	12	Water Shrew	11
Common Snipe	12	Western Tanager	11
Creeping Vole	12	White-headed Woodpecker	11
Double-crested Cormorant	12	Yellow-rumped Warbler	11
Golden Eagle	12	American Pipit	10
Golden-crowned Kinglet	12	American Redstart	10
Gopher Snake	12	Band-tailed Pigeon	10
Gray-crowned Rosy-Finch	12	Common Yellowthroat	10
Heather Vole	12	Dusky Flycatcher	10
Hermit Thrush	12	Fringed Myotis	10
Hoary Redpoll	12	Gray Flycatcher	10
Lewis' Woodpecker	12	Greater Yellowlegs	10
Long-tailed Duck	12	Hammond's Flycatcher	10
Macgillivray's Warbler	12	Horned Lark	10
Northern Hawk Owl	12	House Wren	10
Northern Mockingbird	12	Lapland Longspur	10
Northern River Otter	12	Lesser Yellowlegs	10
Orange-crowned Warbler	12	Long-eared Owl	10
Pygmy Nuthatch	12	Long-tailed Vole	10
Red Fox	12	Merriam's Shrew	10
Red-eyed Vireo	12	Northern Saw-whet Owl	10
Red-tailed Hawk	12	Osprey	10
Red-winged Blackbird	12	Painted Turtle	10
Spruce Grouse	12	Pied-billed Grebe	10
Townsend's Solitaire	12	Pileated Woodpecker	10
Vagrant Shrew	12	Pygmy Shrew	10
Warbling Vireo	12	Racer	10
Water Vole	12	Surf Scoter	10
Western Bluebird	12	Three-toed Woodpecker	10
White-winged Crossbill	12	Townsend's Big-eared Bat	10
White-winged Scoter	12	Violet-green Swallow	10
Willow Flycatcher	12	White-footed Vole	10
Yellow-breasted Chat	12	Wilson's Warbler	10
American Bittern	11	Yellow Warbler	10
American Kestrel	11	American Dipper	9
Bank Swallow	11	American White Pelican	9
Barn Swallow	11	Anna's Hummingbird	9
Big Brown Bat	11	Barn Owl	9
Cliff Swallow	11	Black-chinned Hummingbird	9
Common Loon	11	Blackpoll Warbler	9
Downy Woodpecker	11	Bobolink	9
Meadow Jumping Mouse	11	California Myotis	9
Moose	11	Calliope Hummingbird	9
Mountain Bluebird	11	Coeur d'Alene Salamander	9
Night Snake	11	Cooper's Hawk	9
Red-throated Loon	11	Flammulated Owl	9
Rocky Mountain Tailed Frog	11		

Great Horned Owl	9	Semipalmated Plover	8
Hairy Woodpecker	9	Semipalmated Sandpiper	8
Little Brown Myotis	9	Short-billed Dowitcher	8
Long-legged Myotis	9	Short-eared Owl	8
Mountain Lion	9	Stilt Sandpiper	8
Mourning Dove	9	Vaux's Swift	8
Mute Swan	9	Western Rattlesnake	8
Northern Flicker	9	Western Sandpiper	8
Northern Goshawk	9	Western Screech-owl	8
Northern Rough-winged Swallow	9	Western Small-footed Myotis	8
Pacific Loon	9	Western Wood-pewee	8
Pallid Bat	9	Brown Creeper	7
Prairie Falcon	9	Canyon Wren	7
Pygmy Short-horned Lizard	9	Common Shrew	7
Ross's Goose	9	Ermine	7
Rufous Hummingbird	9	Gyr Falcon	7
Solitary Sandpiper	9	Harlequin Duck	7
Swainson's Hawk	9	Mountain Goat	7
Townsend's Warbler	9	Northern Waterthrush	7
Western Jumping Mouse	9	Preble's Shrew	7
Western Meadowlark	9	Rock Wren	7
Western Skink	9	Rough-legged Hawk	7
Yellow-headed Blackbird	9	Spotted Bat	7
Yuma Myotis	9	Western Long-eared Myotis	7
Alder Flycatcher	8	White-throated Swift	7
American Golden-Plover	8	Winter Wren	7
Baird's Sandpiper	8	Boreal Owl	6
Bighorn Sheep	8	Common Poorwill	6
Black-backed Woodpecker	8	Lynx	6
Black-bellied Plover	8	Merlin	6
Bobcat	8	Northern Bog Lemming	6
Dunlin	8	Northern Long-eared Myotis	6
Dusky Shrew	8	Northern Pygmy-owl	6
Eurasian Wigeon	8	Turkey Vulture	6
Great Gray Owl	8	Black Swift	5
Greater Scaup	8	Common Nighthawk	5
Hoary Bat	8	Peregrine Falcon	5
Least Sandpiper	8	Snowy Owl	5
Loggerhead Shrike	8	Wolverine	5
Long-billed Dowitcher	8	Grand Total	4766
Long-tailed Weasel	8		
Marsh Wren	8		
Northern Alligator Lizard	8		
Northern Harrier	8		
Northern Shrike	8		
Olive-sided Flycatcher	8		
Pectoral Sandpiper	8		
Rock Dove	8		
Rubber Boa	8		
Sanderling	8		

