

Abstract No: A-171

**WETLANDS AS KEYSTONE ECOSYSTEMS: CONSERVATION CORNERSTONES IN DYNAMICALLY-CHANGING LANDSCAPES**

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*MacEwan University, Edmonton, Alberta T5W 4H3, Canada**Corresponding author: lockyd@macewan.ca***SUMMARY**

Ecosystems are interconnected to each other in a web of patches, some of which may be more important regionally than others. These are as keystone ecosystems, ecosystems which have an impact on the landscape inordinate to their size or distribution. Keystone ecosystem evolved from the antecedent keystone species concept and the associated keystone processes model. While these concepts share similar characteristics as with keystone species, the keystone ecosystem concept requires refinement. Wetlands were first introduced as keystone ecosystems in Alberta by Locky (2011). In addition to functioning as distinct ecosystems unto themselves, wetlands are critical conduits between upland and aquatic ecosystems on a heterogenous landscape. Wetlands, like other keystone ecosystems, influence the landscape by two primary but not mutually exclusive pathways: shaping landscape disturbance regimes and providing limited resources on the landscape (DeMaynadier and Hunter 1994). They can survive fire and often remain unlogged, both cases equally providing reliable oases in seas of disturbance. Their resilience on the landscape places them in the role of conduits between different ecosystem types. Peatlands similarly modify and store carbon. Important facets of keystone wetlands as keystone ecosystems include values and societal benefits related to conservation, like carbon storage. However, it is clear that the strong functional linkages between wetlands and other landscape types suggest that negative consequences of wetland loss and impairment are exported far beyond geographic boundaries. Addressing wetland losses and conserving existing wetlands through policy provides value far and above the spatial extent on the landscape (Stoneman *et al.* 2016). When identified and mapped, keystone ecosystems can provide politicians, managers, planners, and the public useful information about critical ecosystem components (Stohlgren *et al.* 1997). Uniquely, this is where ecology and management become one. The planning process can be fortified with knowledge of keystone ecosystems. Conversion and or loss of critical functions and values can thus be avoided, particularly for long-term planning. In the case of Alberta, wetlands are found in all of the province's biomes and provide a wide range of ecosystem functions and properties. Wetlands have been subjected to a variety of anthropogenic impacts, including climate change (Locky 2011, 2012, Stoneman *et al.* 2016). Conservation and enhancement of wetlands leverages ecological and societal benefits far above the areal extent of the wetland and far beyond a wetland's borders.

**Keywords:** *conservation, function, keystone ecosystem, peatland, policy, value, wetland*

**INTRODUCTION**

The antecedent concept of keystone ecosystem is keystone species which was first by Paine (1966) during his work on the role of *Pisaster* in intertidal communities. The removal of this top predator but non-dominant species, from the community led to the collapse of the system, reducing diversity from 15 to 8 species. The keystone species concept emphasizes direct control processes like competition and predation rather than indirect processes like nutrient cycling in the control of biodiversity. There are also keystone guilds or groups of species that fill various roles, including fruit trees providing fruit to frugivores in seasons with less resources, and certain mammals and birds critical to dispersal of certain seeds and other organisms providing critical landscape disturbances, like beavers and alligators (see review in DeMaynadier and Hunter 1997). Keystone processes are those that are fundamental to the maintenance of an ecosystem (Vold and Buffet 2008). These could include fire in maintaining open ponderosa pine forests and grasslands in B.C.'s dry interior or pollination in maintaining biological productivity (Kevan 1991). Similarly, ecosystems which have a positive impact on the landscape inordinate to their size or distribution are called keystone ecosystems.

Examples of keystone ecosystems include wild coffee ecosystems (Goel *et al.* 2001), coastal temperate rainforests (Moola *et al.* 2004), riparian areas (Naiman *et al.* 2005), estuaries (Pojar 2003), some lakes and other aquatic ecosystems (Ocean Partners, Internet), mangroves (National Geographic 2001), freshwater deltas (Lesak 2014), and coral reefs. Using coral reefs as an example, while our understanding of their role as a keystone

ecosystem is incomplete, there is evidence that coral reefs provide a keystone role within the marine environment (Hagedorn and Spindler 2014). While they only encompass 0.2% of the earth's surface over one-quarter of all marine life exists on a coral reef at some point during their life cycle. The proportion of coral reefs threatened with extinction has exceeded that of terrestrial ecosystems (Hagedorn and Spindler 2014). Additionally, coral reefs are among the oldest and most diverse of ecosystems. Wetlands only cover approximately 6% of the earth's surface, of which half are peatlands, but unlike coral reefs, are found in most terrestrial biomes in some form.

Locky (2011) first highlighted wetlands as keystone ecosystems in Alberta using function and value in terms of their limited proportional representation on the landscape; wetlands are found in every biome within the province and likely contribute services and value inordinate to their size on the landscape. Specific attributes and properties of wetlands as keystone ecosystems have yet to be quantified and qualified.

## METHODS

Using Locky (2011, 2012) and the literature and white papers, this research attempts to fortify the concept of wetlands as keystone ecosystems using examples from Alberta and elsewhere.

## RESULTS AND DISCUSSION

Wetland conservation has been recently gaining worldwide momentum and scientific evidence supports the dual paradigm of wetlands as providing ecological function and economic value (Stoneman *et al.* 2016). Determination of function and value are elusive qualities for many ecosystems. Costanza *et al.*'s (1997) seminal manuscript outlining the value of the world's ecosystem services and natural capital highlights the significance of ecosystem services and values of wetlands relative to other ecosystem types. The research suggests that wetlands are worth more than most other of the earth's ecosystems, approximately \$20,000/ha/year.

While not all wetlands perform all functions nor do they perform all functions equally well, it is well known that valued wetland functions include flood control, groundwater recharge/discharge, sediment and nutrient retention, climate change mitigation, biodiversity reservoirs, wetland products, recreation and tourism, and cultural/heritage value (Locky 2011). The presence of keystone ecosystems on the landscape sustain natural ecosystem process and scarce resources (adapted from Stohlgren *et al.* 1997, deMaynadier and Hunter 1997). They are the parts of the landscape that have high diversity, distinctive species compositions, and/or distinctive ecological processes that are beneficial to many other species and/or ecosystems. Keystone ecosystem presence and arrangement often determines the nutrient balance of a region (Blaschke 2005) in addition to a vast array of other functions and values.

As wetlands are generally minor components on the landscape wetlands fulfil the criteria of being critical keystone ecosystems (Locky 2011, 2012) that function as conservation cornerstones.

### *Keystone Species, Processes, and Ecosystems*

DeMaynadier and Hunter (1997) first introduced the keystone ecosystem concept as a means to capture biotopes having greater importance to the biological structure and function than the average landscape unit. Thus, the definition is extended such that species in ecosystems is upscaled to the role of ecosystems on the landscape. Like keystone species, the concept of keystone ecosystems can be vague and inconsistent. Similarly, as many species have been non-rigorously identified as keystone around the world to the point of meaning 'important-for-something', vis-a-viz functional importance vs. keystone-ness (Hurbert 1997), even less rigour has been applied to identifying keystone ecosystems. Indeed, Mouquet *et al.* (2013) outline that while some communities in nature contribute disproportionately to regional dynamics, the concept of keystone ecosystem needs to be refined. This is important to understand species interactions in space and ultimately, produce a better understanding of the consequences of habitat loss.

### *Keystone Ecosystem Mechanisms*

Ecosystems are linked to each other in complex web of interconnected patches and a minority of these may be more important regional than others, functioning as keystone ecosystems (Mouquet *et al.* 2013). Keystone ecosystems influence landscapes by two primary mechanisms: 1) shaping landscape disturbance regimes or 2) providing a limiting resource on the landscape. Many key aspects of wetland could simultaneously fit within both of these categories, i.e., are not mutually exclusive, but I have separated them into disturbance regimes and provision of limiting resources for convenience.

### *Disturbance Regimes*

Many wetlands, including forested peatlands, are left on the landscape during logging operations. The author's work in boreal Canada as related to Locky and Bayley (2007) strongly demonstrated how these remnant peatlands, at times completely encircled by clear-cut forest, appeared to maintain perfect hydrological function with

intact plant communities for at least 12 years post-harvest (Figure 1A). The resilience is due to the complex hydrological connections which maintain the wetland function. These remnant forested wetlands are literally oases in a sea of cut forest, resilient to adjacent landscape disturbances while themselves providing resources to vertebrates, invertebrates, and possibly other organisms that may have been displaced by the disturbance.



Figure 10: Wetlands as oases to disturbance on the landscape in Canada. A: Forested wetlands left on a logged landscape in boreal Manitoba. B: Spring slope fen in midst of fire-impacted landscape on boreal Alberta. Image A by Louisiana-Pacific Ltd, Image B by D.A. Locky.

Many wetlands can survive forest fires and eventually function as oases for organisms in a greatly changed landscape. Spring slope fens are found intermittently in the Boreal Plains forest of western can. Often very small in nature, their unique hydrology allows them apportion a degree of reliability unseen in other wetland and aquatic ecosystems. Despite their small size it is not uncommon that they survive forest fires virtually intact (Figure 1B). Similar to self-sustaining peatland remnants in logged forests, these sites function as oases for various organisms on the landscape.

During the drought of the 2000s in western Canada, ducks which would normally be breeding in the now dry prairie potholes migrated north to still wet boreal marshes as part of the peatland complexes (Author's observations, Abraham 2014). This is referred to as waterfowl displacement. In this case, one wetland type was providing relief for the loss/degradation of another wetland type. Riverine and lacustrine wetlands can provide relief from disturbance by their ability to buffer the adjacent landscape from the effects of not only high water levels, but low water levels.

#### *Provision of Limiting Resources*

Wetlands provide a plethora of limiting resources to adjacent ecosystems/organisms. Not unlike coral reefs (Hagedorn and Spindler 2014), coastal marshes like *Spartina* salt marshes providing primary productivity and nursery habitat (Pomeroy and Wiegert 1981), springs wetlands Keystone ecosystem presence and arrangement often determines the nutrient balance of a region (Blaschke 2005).

Of particular importance are riparian ecosystems near streams, lakes and wetlands as they cover a relatively small area yet support a disproportionately large number of species (Naiman *et al.* 2005). In many parts of the world, such as the boreal zone, riparian areas are comprised primarily of wetlands (Locky 2011).

Ephemeral wetlands are increasingly being accepted as critical landscape components (Cohen *et al.* 2015), with diverse and important flora (Zedler 2003, Deil 2005). Ephemeral wetlands have been well-known to provide critical refugia in drier landscapes such as the vernal pools in California (Zedler 2003). However, the importance of ephemeral wetlands as providing critical services is less accepted in other jurisdictions where they may be just as important as more permanent wetlands (Locky 2011, Stoneman *et al.* 2016). With respect to disturbance regimes, wetlands provide critical refugia to organisms during natural (and non-natural) disturbance events such as fire (Bergeron 1991) and logging (Locky and Bayley 2007).



Figure 11: Ephemeral wetlands (dark patches) in late spring in southern Alberta, Canada. These wetlands provide an important source of habitat for invertebrates and vertebrates and function as recharge conduits for ground water. Image by D.A. Locky.

Wetlands also store resources of significance to humans: carbon. For example, Alberta's peatlands hold 11% of Canada's soil carbon and sequester more carbon than the forests and the value of this carbon is of strategic economic importance (Anieski 1998). Peatland conservation plays a potential role in ameliorating climate change

#### *Conservation Cornerstones*

The proportion of coral reefs threatened with extinction has exceeded that of terrestrial ecosystems (Hagedorn and Spindler 2014) and this is arguably similar to the case of wetlands. Research has shown that when keystone ecosystems are lost from the landscape matrix there may be serious consequences for the whole region (Erikson 2014). For example, it is estimated that as of 1999, the cumulative value of Alberta's lost wetlands was \$45.7B (Wilson *et al.* 2001). Like keystone species, conservation of keystone ecosystems plays a critical role in maintaining integrity of the larger landscape (deMaynadier and Hunter 1994). Lost wetlands represent a potential lost legacy far greater than their extent on the landscape given their status as keystone ecosystems. As keystone ecosystems, wetlands are truly conservation cornerstones.

#### **CONCLUSION**

Ecosystems are linked to each other in complex web of interconnected patches. Some of these patches may be more important regional than others, functioning as keystone ecosystems. Wetlands are ideal keystone ecosystems that influence landscapes by shaping landscape disturbance regimes or providing a limiting resource on the landscape. Enhancement of wetland protection and conservation will leverage the benefits of their keystone function, thus wetlands are critical conservation cornerstones.

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