Mammal Review

Mammal Review ISSN 0305-1838

REVIEW

Ecosystem services provided by beavers *Castor* spp.

Stella THOMPSON* *Department of Forest Sciences, University of Helsinki, Latokartanonkaari 7, 00790, Helsinki, Finland. Email: stella.thompson@helsinki.fi*
Mia VEHKAOJA *Department of Forest Sciences, University of Helsinki, Latokartanonkaari 7, 00790, Helsinki, Finland. Email: mia.vehkaoja@helsinki.fi*
Jani PELLIKKA *Natural Resources Institute Finland, Latokartanonkaari 9, 00790, Helsinki, Finland. Email: jani.pellikka@luke.fi*
Petri NUMMI *Department of Forest Sciences, University of Helsinki, Latokartanonkaari 7, 00790, Helsinki, Finland. Email: petri.nummi@helsinki.fi*

Keywords
ecosystem services, Eurasian beaver *Castor fiber*, meta-analytical function transfer, monetary valuation, North American beaver *Castor canadensis*, Northern Hemisphere, payments for ecosystem services

*Correspondence author

Received: 29 May 2018
Accepted: 26 May 2020
Editor: DR

doi: 10.1111/mam.12220

ABSTRACT

1. We aimed to recognise beaver-produced ecosystem services and quantify their theoretical value for the entire Northern Hemisphere. Activity of the Eurasian beaver *Castor fiber* and the North American beaver *Castor canadensis* in the landscape provides ecosystem services and disservices. Services produced by beaver activity include water purification, moderation of extreme events, habitat and biodiversity provision, nutrient cycling, greenhouse gas sequestration, recreational hunting and fishing, water supply, and non-consumptive recreation. Beaver-produced services have not been compiled, analysed, or quantified previously.
2. Each service we evaluated is worth millions to hundreds of millions of US dollars (USD) annually. Habitat and biodiversity provision (133 million USD), along with greenhouse gas sequestration (75 million USD), are particularly valuable services in absolute terms, while non-consumptive recreation (167 USD ha^{-1}) and habitat and biodiversity provision (133 USD ha^{-1}) have the largest annual per-hectare values.
3. Our results can be used to broaden decision-making and management perspectives, as we offer value estimates to wildlife managers and municipality planners for assessing local site-specific beaver wetland values and the opportunities for their realisation. Implementing Payments for Ecosystem Services schemes offer a concrete way for societies to benefit from beaver-produced services while concurrently compensating beaver-produced losses accrued to landowners. Building such schemes offer long-term realisation of ecosystem services and damage mitigation. This would lead to increased societal well-being and increased conservation interest and efforts.

INTRODUCTION

Various ecosystem functions and products, such as clean air, water, and food, are conditions and processes necessary or beneficial to humans (Millennium Ecosystem Assessment 2005a) and are referred to as ecosystem services. Ecosystem services directly or indirectly sustain humans, as they are necessary for the functioning of societies and for the ability of ecosystems to absorb unwanted by-products of economic production (Boyd & Banzhaf 2007). Ecosystem services are environmental assets that may be actively or passively gained, consumed, used, and enjoyed. The MEA divides the services into four categories according to their functions and benefits: regulating, provisioning, supporting, and cultural (MEA 2005a).

Many environmental assets are currently being depleted and degraded at rates more rapid than their renewal. As several environmental assets are crucial to the balanced functioning of societies, their conservation has become a priority. However, as long as ecosystem services remain outside of economic markets, no fiscal incentives are in place for their conservation (Farley & Costanza 2010). This has created a need for their monetary valuation, to aid policy- and decision-makers. Economic valuation using commensurate monetary or other measures is necessary for decision-makers assessing the effects of various ecosystem services and the outcomes of their utilisation (Liu et al. 2010). Once valuation is complete, preservation of the produced benefits is next on the agenda. Several mechanisms exist for this, such as Payment for Ecosystem Services schemes (Ezzine-de-Blas et al. 2016), in which economic processes are used to incentivise resource managers (e.g. landowners) to uphold an existing ecosystem service on their land in return for monetary benefits from a beneficiary (e.g. a nearby community or industrial factory). The schemes compensate for conservation-related losses accrued to resource managers. Currently, schemes for wetlands or water management are in place for, e.g. carbon storage, storm-water management, nutrient recycling, and water filtration in, e.g. France, the USA (Oregon), and the UK (e.g. Guillozet 2015). Beaver (*Castor* spp.) wetlands provide all of these services, but so far no Payment for Ecosystem Services schemes have been implemented in these areas.

Beavers and their ecosystem engineering are natural components of freshwater wetlands in the Northern Hemisphere (Johnston 2017). These wetlands have co-evolved along with the species. Beavers modify their surroundings and influence succession, potentially leading to novel ecosystems, such as beaver wetlands and beaver meadows, with unique habitat characteristics. Beaver occupancy forms new habitats (Whitfield et al. 2015), as beavers strongly affect the structures and functions of ecosystems and concurrently provide ecosystem services for humans through their habitat modification. Increasing beaver populations may also increase the future value of the services they provide. The Eurasian beaver *Castor fiber* and the North American beaver *Castor canadensis*, both included in this review, are classified as Least Concern according to the International Union for Conservation of Nature.

Much is known of the physical and ecological alteration that beaver activity causes, and beaver activity has been studied extensively from an ecological perspective. However, we aim to take a utilitarian viewpoint and assess beaver ecosystem engineering through the human-centred ecosystem services approach that focuses solely on the benefits of nature for humans. This allows us to look at how societies may benefit from or endure beaver activity. No previous quantification has been performed for the magnitude and value of the effects of beavers and how they directly or indirectly reflect onto individual stakeholders or societies. From an ecological perspective, beavers do not damage or negatively influence their surroundings (except for in areas in the Southern Hemisphere where the North American beaver is invasive), but from an ecosystem services viewpoint, damage (i.e. disservices) to humans does occur. In our assessment, many of these effects appear as disservices at the stakeholder level (e.g. beaver-induced flooding of forests) while simultaneously emerging as services to society at large (e.g. upholding water supplies; Bhat et al. 1993, Siemer et al. 2013). The ecosystem services approach is limited, as it does not consider how humans in turn have degraded and narrowed the behaviour and function of organisms in their natural habitats.

We formulate direct and indirect impact chains of beaver action leading to human well-being using existing data. We use the ecosystem services frame to identify the key chains producing the services; these impact chains are relevant focal points for future management options. We do this by quantifying preliminary estimates of current Northern Hemisphere freshwater mineral soil wetland and beaver values. Data valuing disservices are scarce and dated, and we therefore concentrate solely on describing and quantifying the services that are provided by beavers. Our aim with this utilitarian focus is to broaden current decision-making and management perspectives, which could aid in regulating and utilising beaver activity to help maximise societal well-being and lead to increased conservation efforts and further research. We approach this aim by producing estimates based on values found in the literature, to achieve a first and theoretical attempt at valuing ecosystem services provided by beavers.

METHODS

As our study relates to beaver wetlands, we first gained insight into global wetland resources and their valuation (e.g. Schuyt & Brander 2004, Ramsar Convention on Wetlands 2018). The value of wetlands has long been debated, and they are currently valued for a multitude of reasons and needs (MEA 2005a). Foremost, it is important to understand how to maximise the benefits and turnarounds gained from wetland habitats, while upholding a trade-off or balance between these gained values and conservation actions conducted and/or damages incurred (Gustavson & Kennedy 2010).

We used the ecosystem services categorisations for wetlands in Haines-Young and Potschin (2018), MEA (2005b) and Russi et al. (2013) to determine which services beavers provide in the Northern Hemisphere (Table 1 and Fig. 1). Service-specific valuation was required to gain an idea of how valuable individual ecosystems are to societies. Valuation methods aim to bridge economic and environmental accounting, making the monetary valuation of ecosystem services, and thereby decision-making concerning them, more straightforward.

Table 1. Ecosystem services provided by beavers in the Northern Hemisphere and their categories, along with the number of approved value estimates found for each service during the database and literature searches; this number of value estimates was used in the meta-analytical function transfer. The abbreviated name of each variable as used in meta-analytical function transfer is indicated in parentheses

Ecosystem service	Ecosystem service category	Number of value estimates
Moderation of extreme events (FloodDrought)	Regulating	11
Greenhouse gas sequestration (GHG)	Regulating	8
Water purification (Quality)	Regulating	26
Water supply (Supply)	Provisioning	6
Recreational hunting and fishing (HuntFish)	Provisioning	3
Habitat and biodiversity provision (HabBio)	Supporting	8
Nutrient cycling*	Supporting	0
Non-consumptive recreation (Recreation)	Cultural	17
Historical value*	Cultural	0

*Our search provided no service value, so this ecosystem service was left out of our analyses.

Database search and literature review

We searched for relevant literature in seven ecosystem valuation databases (Appendix S1) and found relevant studies in two: the Environmental Valuation Reference Inventory database and The Economics of Ecosystems and Biodiversity – Valuation Database. We used ResearchGate and Web of Science to search for additional relevant literature using the word "beaver" combined with terms such as "ecosystem services", "flooding", "carbon balance", "methane", "mercury", "nutrients", "biodiversity", "water", and the word "wetlands" coupled with "value", "valuation", and "ecosystem services". The following inclusion criteria were applied to the documents found in all searches: all documents (1) concerned freshwater mineral soil wetlands in the Northern Hemisphere, (2) only incorporated specific wetland ecosystem services, (3) involved primary research, to avoid double counting, and (4) were published between 2000 and 2018. The database search was conducted between 15 and 18 October 2018. Our literature search only incorporated general freshwater mineral soil wetlands located between the northern and southern latitude limits (69°N and 26°N) of the Northern Hemisphere beaver range, because we wished to ensure that our results would not be overestimated due to value estimates from ecosystems and climates outside of the beaver range.

We examined the whole documents to ensure they contained all relevant information needed for our analysis, i.e. information on currency year, type of valuation method, size of the study area, and study and area population when applicable (i.e. for willingness-to-pay studies). If a

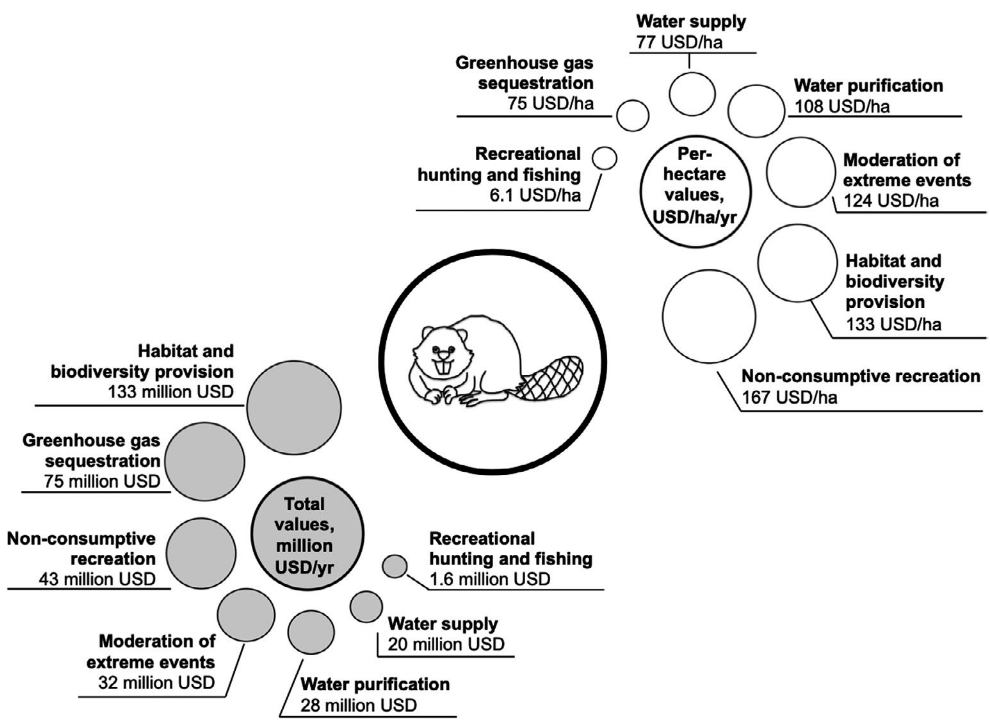

Fig. 1. Values of ecosystem services produced by beaver ponds, given in annual per-hectare values (white circles) and aggregated over the one million ha Northern Hemisphere beaver range per year (grey circles). Circles are not to scale.

study did not specify the exact surface area but defined an exact location (e.g. an entire country or a specific county or municipality), we searched online for information on surface area. All documents we accepted were written in English. We included estimates from the documents using contingent valuation, choice experiment, travel, replacement or avoidance cost, or market price methods, and all values were converted into annual values per hectare.

Beaver population and beaver wetland area

We examined the Northern Hemisphere, covering boreal, temperate forest, temperate grassland, and chaparral regions in North America and Eurasia (Europe and Russia). We used beaver range maps in Touihri et al. (2018) and Halley et al. (2012) to narrow our search and analyses to cover only the current approximate combined geographic range of both beaver species, which was located between 69°N and 26°N. North American beaver populations appear to be stable, so we used the lower bound estimates for population (9.6 million), colony number (2.4 million colonies) and pond area (928900 ha) for North America, as reported by Whitfield et al. (2015). The beaver populations in several countries of Eurasia are increasing, so we used the population estimate (1.5 million individuals) in Halley et al. (2021). The combined North American and Eurasian estimates raised the total Northern Hemisphere population to 11.1 million individuals. Colony numbers and pond area estimates for Eurasia were calculated using the 1.5 million individual population estimate to recalculate the Eurasian values in Whitfield et al. (2015). They incorporated differences in pond-building frequencies and dam numbers between the two beaver species, which is why we felt comfortable basing our estimates on the study. However, the pond area estimate in Whitfield et al. (2015) only included dam-building beavers. Beavers inhabit varying habitats from riverine to open water areas, and the degree to which they build dams and create ponds varies due to habitat characteristics. The percentage of beavers that build dams has been studied in several countries. Some studies show a similar percentage for both species (e.g. Danilov & Fyodorov 2015: Eurasian 74% vs. North American 77%), while others suggest that Eurasian beavers dam less frequently (e.g. Zav'yalov 2011: Eurasian beaver 10–63%; Whitfield et al. 2015: North American beaver 50–80%). Our valuations focus on dam-building beavers, which, according to these estimates, make up 49–69% of the beaver population. We are aware that the services provided in various beaver habitats may differ to some extent from each other. Also, individual beavers are not strictly dam-builders or non-dam-builders, but rather build dams depending on the situation. However, damming does appear to be common in both species. We have compiled our calculations assuming that half of the Northern Hemisphere beaver population builds dams at any given time.

Meta-analytical function transfer of beaver wetland values

We performed a meta-analytical function transfer, where wetland values from primary valuation studies were compared against "various covariates relating to policy site characteristics and research design choices made by authors" (Chaikumbung & Scarborough 2016). As the method utilises values from several previous studies and study sites, a greater variety of ecosystems and site conditions may be incorporated into the calculations (Brander 2006), which potentially increases the validity estimated over large geographic areas. We transferred the values from the ecosystem services valuation studies we collected, using the meta-analytic regression model given in Equation 1.

$$\ln y_{ij} = \gamma ES_{ij} + \beta^b X^b_{ij} + \beta^s X^s_{ij}, s \quad (1)$$

where y_{ij} was the monetary value of a wetland in US dollars (USD) per hectare per year, ES included the ecosystem services provided by a beaver wetland, X^b was a vector describing wetland type, and X^s was a vector describing the study characteristics (i.e. survey method). Subscript i was the number of studies (i = 1 … 44), and subscript j is the number of observations (j = 1 … 75). Vectors β^b, β^s, and γ contained coefficients to be estimated for the explanatory variables X^b, X^s, and ES, respectively. We used ordinary least squares regression for the estimation. The dependent variable was the natural logarithm transformation of the annual per-hectare USD value for each wetland.

First, we standardised price values from various countries and years into comparable values. To do this, we used purchasing power parity adjusted exchange rates to convert the various currencies from our valuation study sites into USD at 2017 price levels. This controlled for differences in price levels between countries. To adjust prices to account for inflation, we used gross domestic product inflators from the World Bank (2018) as in Brander (2006). We then calculated their relative values as the real value of each service.

These values were next used in the function transfer. The resulting coefficients for ɣ indicated the "direction and magnitude of the effect of each explanatory variable on the unit value of wetland ecosystem services" (Brander 2006). We then calculated the exponentials for the coefficients, i.e. annual per-hectare values for each service, and combined them with the beaver wetland area estimate we had calculated. This formed an aggregated magnitude estimate of individual ecosystem services provided by beavers for the entire Northern Hemisphere. Most wetland meta-analyses have included wetlands from around the world, while ours only incorporated wetlands in beaver habitats in the Northern Hemisphere. With this, we hoped to avoid overestimations in ecosystem service values that could be caused by differences in Northern and Southern Hemisphere wetlands.

Geographic information system analysis

Ecosystem services relate to human demand and need; a service remains only potential until a society requires or covets it, at which point the potential service becomes real (Grunewald & Bastian 2015). No studies have assessed the required proximity of beaver wetlands to human habitation in relation to ecosystem services, and conducting a thorough analysis of geographic proximity to determine this was beyond the scope of our study. However, to avoid completely disregarding this aspect, we roughly analysed the percentage of beaver wetland area coinciding with three human population density classes (sparse population: 1–199 people per km^2; moderate population: 200–999 people per km^2; dense population: 1000+ people per km^2). The resulting percentages were then used as human population density coefficients in our calculations (hereafter termed ‘density coefficient’). The value of locally functioning ecosystem services was calculated using only the percentage of beaver wetland area where human habitation was dense or moderate; i.e., the percentage of sparse human habitation was left out of the calculations. The areas of the intersecting polygons for calculating the coefficients were computed using QGIS 2.18. The global land cover map (ESA GlobCover 2009) was used for the wetland data, and the 2015 data from the Gridded Population of the World, v4.10 (Center for International Earth Science Information Network 2017) were used for the human population data.

RESULTS

Our database search produced 105 documents fulfilling the four inclusion criteria (see ‘Database search and literature review’ above). After examining each of these documents for relevant information, we ended up with 43 utilisable documents (articles, grey literature texts, reports, books); 75 individual value observations were obtained from these documents. Studies and reports were found from 14 countries. Sixty-three per cent (27 texts) of the documents were from Europe, 37% (16 texts) from North America, and none from Russia. Studies were spread across four biomes: temperate forest (23 texts, 52%), boreal forest (9 texts, 20%), temperate grassland (6 texts, 14%), and chaparral (4 texts, 9%), while 5% (two texts) spread over both the boreal and temperate forest zones. The studies identified the study habitat as lacustrine (14%), riverine (18%), or urban (9%) wetlands, while a majority (61%) of the studies either incorporated several wetland types or did not specify the habitat. These we clumped together as general freshwater wetlands. A list of the documents used in our final beaver wetland valuation can be found in Appendix S2. The most common reason for discarding a document was that it did not provide information on the currency year a study used, so that we were unable to calculate purchase power parities for the values provided. We did not find utilisable value estimates filling all our inclusion criteria for nutrient cycling or historical value (a ‘cultural’ service), so our final meta-analytical function transfer included values for the following ecosystem service variables (see Table 1): moderation of extreme events (variable FloodDrought), greenhouse gas sequestration (GHG), water purification (Quality; all services in the ‘regulating’ category), water supply (Supply), recreational hunting and fishing (HuntFish; both ‘provisioning’ services), habitat and biodiversity provision (HabBio; a ‘supporting’ service), and non-consumptive recreation (Recreation; a ‘cultural’ service).

Northern Hemisphere beaver wetland resources, meta-analytical function transfer, and geographic information system analysis

The total beaver population is increasing in the Northern Hemisphere (Gibson & Olden 2014, Whitfield et al. 2015, Halley et al. 2021). Current Northern Hemisphere population estimates and dam-building beaver wetland area estimates are shown in Table 2. We used these values as the basis for calculating all other estimates in our study, and the area estimate was also used for scaling up our meta-analytical function transfer results. Table 3 presents the mean and standard deviations for the ecosystem service values, and Table 4 presents the results of our meta-analytical value transfer.

None of the ecosystem services differed significantly from the others; i.e., none of the services was valued exceptionally high or low in the meta-regression, probably because we only included Northern Hemisphere studies that were located between the northern and southern latitude limits of the beaver range (69°N and 26°N). For example, habitat and biodiversity provision and recreational hunting and fishing services may be valued more highly in the tropics, which are not included

Table 2. Beaver population and colony estimates, and estimates for beaver pond area in the Northern Hemisphere. Estimates were calculated by extrapolating data from Whitfield et al. (2015) and Halley et al. (2021)

	Europe and Russia	North America	Total Northern Hemisphere
Beaver population	1.5 million	9.6 million	11.1 million
Total number of beaver colonies	242000–405000	1.5–2.6 million	1.8–3.0 million
Number of dam-building colonies			895000–1.5 million
Beaver pond area, ha	24600–181000	928900	952600–1109000*

*Rounded to 1 million ha in our calculations.

Table 3. Definition and description of the dependent variable and explanatory variables used in the meta-regression model. Mean values for each variable indicate the mean value per hectare per year given in US dollars standardised to the year 2017. For the dependent variable, the mean is given as the natural logarithm

	Variable	Mean	Standard deviation
Dependent variable	Wetland value, USD(2017) ha^{-1} yr^{-1} (ln)	7.152	8.263
Wetland variables			
Ecosystem services	Greenhouse gas sequestration (GHG)	1.462	0.891
	Moderation of extreme events (FloodDrought)	1.973	0.827
	Water supply (Supply)	1.160	1.099
	Water purification (Quality)	1.795	1.426
	Habitat and biodiversity provision (HabBio)	1.882	1.012
	Recreational hunting and fishing (HuntFish)	1.811	1.273
	Non-consumptive recreation (Recreation)	2.137	1.091
Wetland type	General freshwater wetland	1.609	1.121
	Lacustrine wetland	1.833	0.581
	Riverine wetland	2.466	1.513
	Urban wetland	2.880	0.155
Study variables			
Valuation method	Contingent valuation	1.374	1.258
	Choice experiment	2.474	0.887
	Travel cost method	1.561	0.862
	Avoidance cost	2.175	0.921
	Replacement cost	3.797	0.544
	Market prices	1.666	0.660

in our dataset. This may lead to aggregation bias in our data, where the mean values of individual variables are similar between different studies (Borenstein et al. 2009, Deeks et al. 2019). While substantial variation may occur within a study, the meta-regression uses study-level means to summarise data, and therefore, relationships between an explanatory variable (i.e. meta-regression variable) and the outcome variable may not become apparent. Pre-defined study weighting in the meta-regression also causes larger studies to have more pronounced effects on the coefficients (Deeks et al. 2019). Coefficient significance shows a linear relationship between the explanatory and outcome variables. The model is semi-logarithmic, so the correct annual per-hectare values for individual services are calculated by taking the exponentials of the related meta-regression coefficients in Table 4.

We used contingent valuation as a reference method in the meta-regression and obtained significant results for four (contingent valuation, travel cost, replacement cost, and market price methods) of the six valuation methods assessed in the model. Other meta-analyses have previously determined significant differences for three valuation methods (replacement cost: Woodward & Wui 2001; contingent valuation: Brander 2006; travel cost method: Reynaud & Lanzanova 2017), so our results are in line with previous studies. We also assessed the importance of habitat on the valuation results and found that general freshwater habitats produced significantly lower values and urban wetlands produced significantly higher values than the other habitats. Urban wetlands may be valued more highly because they provide nature values in areas with little natural habitat. General freshwater habitats may be significant because most of the studies (61%) in our meta-regression are grouped into this category, and model weighting may cause larger groups to have a stronger effect on the outcome.

Table 4. Estimates of the meta-regression models with random effects. Ordinary least squares results were as follows: adjusted R^2 = 0.231. N = 75. Statistical significance is indicated with ***, **, and * for 1, 5, and 10% levels, respectively

		Variable	Coefficient	p-value
Wetland variables				
	Ecosystem services	Greenhouse gas sequestration (GHG)	4.314	0.816
		Moderation of extreme events (FloodDrought)	4.817	0.661
		Water supply (Supply)	4.342	0.844
		Water purification (Quality)	4.680	0.792
		Habitat and biodiversity (HabBio)	4.887	0.616
		Recreational hunting and fishing (HuntFish)	1.811	0.839
		Non-consumptive recreation (Recreation)	5.119	0.374
	Wetland type	General freshwater wetland	3.085**	0.034
		Lacustrine wetland	3.632	0.251
		Riverine wetland	3.516	0.180
		Urban wetland	2.880*	0.069
Study variables				
	Valuation method	Contingent valuation	2.284***	0.001
		Choice experiment	3.390	0.146
		Travel cost method	2.459**	0.012
		Avoidance cost	3.406	0.144
		Replacement cost	3.796**	0.011
		Market prices	2.886**	0.044

We determined greenhouse gas sequestration (variable GHG) and habitat and biodiversity provision (HabBio) to function at global scales; i.e., their monetary realisation was not strongly or directly influenced by human population density and their human density coefficients are therefore equal to one. On the other hand, moderation of extreme events (FloodDrought), water supply (Supply), water purification (Quality), recreational hunting and fishing (HuntFish), and non-consumptive recreation (Recreation) services function at local scales and are dependent on sufficient human population densities for their utilisation to be feasible. The density coefficient for moderate and dense human population density derived from our geographic information system analysis was 0.26, which was used as the density coefficient for local-level services. Figure 1 and Table 5 show the annual per-hectare values and quantified values of beaver activity over one million ha of beaver ponds in the Northern Hemisphere. The value results in Table 5, and those presented hereafter, relate to the approximately 50% of beavers that build dams. Non-consumptive recreation, habitat and biodiversity provision, and moderation of extreme events had the highest annual per-hectare values (167, 133, and 124 USD(2017) per ha per year), while recreational hunting and fishing was valued the lowest (6.1 USD(2017) per ha per year). However, when combined with the density coefficients, habitat and biodiversity provision, greenhouse gas sequestration, and non-consumptive recreation became the most valuable ecosystem services over the one million ha Northern Hemisphere beaver area.

Regulating services provided by beavers

Moderation of extreme events

Beaver-created wetlands modify natural flow regimes by increasing surface- and groundwater retention, thereby moderating extreme events. Flood peaks are mitigated through rainwater retention and drought conditions by slowly releasing water through dams (Rosell et al. 2005, Westbrook et al. 2006, Burchsted et al. 2010, Gibson & Olden 2014). A single beaver dam may modify the volume of flowing water by 3400–628000 m^3 per annum, depending on ecosystem and water system characteristics (Buckley et al. 2011). Calculating using the lower bound value (3400 m^3) equates to all Northern Hemisphere

Table 5. Annual per-hectare service values and aggregated economic value of beaver wetland ecosystem services in the Northern Hemisphere, calculated using our meta-regression value function, and the density coefficient used to aggregate per-hectare values. Meta-regression variable names are given in parentheses

Ecosystem service	Per-hectare service value USD(2017) ha^{-1} yr^{-1}	Value of ponds created by dam-building beavers (1 million ha) USD(2017) yr^{-1}	Density coefficient used in calculations
Habitat and biodiversity provision (HabBio)	133	133 million	1
Greenhouse gas sequestration (GHG)	75	75 million	1
Non-consumptive recreation (Recreation)	167	43 million	0.26
Moderation of extreme events (FloodDrought)	124	32 million	0.26
Water purification (Quality)	108	28 million	0.26
Water supply (Supply)	77	20 million	0.26
Recreational hunting and fishing (HuntFish)	6.1	1.6 million	0.26

beaver dams attenuating 3–5 billion (10^9) m^3 of water, assuming one dam per beaver colony (895000–1.5 million dam-building colonies in Table 2) at any one time. During slow water flow, a dam may withhold 30–60% of a stream system's water volume (Kay 1994). Contrastingly, increased baseflow decreases the frequency and duration of drought events (Burchsted et al. 2010, Gibson & Olden 2014). Karran et al. (2017) estimated global beaver ponds to store 2.5–11 billion m^3 of water. Hood and Bayley (2008) showed that beaver presence increases the amount of open water in a landscape ninefold during both wet and dry conditions, but see Westbrook et al. (2006, 2011). The economic gain provided by beaver-created wetlands moderating extreme events amounts to 32 million (dam-builders only) USD(2017) per year (Table 5; variable FloodDrought).

Greenhouse gas sequestration

Wetlands act as greenhouse gas (GHG) sinks and sources, either sequestering or emitting carbon, carbon dioxide and methane, and potentially influencing climate change. Beaver activity causes both sink and source dynamics of carbon and methane, which vary due to the temporal and spatial nature of beaver occupancy, along with dam/flood/pond age and water table level (Lazar et al. 2015, Vehkaoja et al. 2015, Nummi et al. 2018). A single beaver wetland may simultaneously both sequester and emit GHGs if several beaver works are concurrently present (e.g. a dry beaver meadow and a deep inundation area).

Beaver meadows, dams, and ponds endure for extended periods of time and may function as depositories for centuries (Persico & Meyer 2009). Beaver inundations contain large levels of dead wood generated by flooding (Thompson et al. 2016, but see also Misiukiewicz et al. 2018), along with trees felled for dam and lodge construction (Johnston 2017). Beaver activity also influences peat formation, which further modifies GHG dynamics (Nummi et al. 2018), although this aspect remains little studied and unclear. Carbon is also stored in the pond sediments. Carbon storage in beaver meadows may reach 8–23% of estimated total landscape carbon storage (Wohl 2013), and may (Johnston 2014, 2017) or may not (Nummi et al. 2018) be great enough to offset the carbon release of beaver ponds. Nummi et al. (2018) calculated this sequestered carbon in beaver ponds globally to equal 378 Tg.

Calculating the net biogeochemical effects of beaver activity is therefore challenging, making it difficult to assess their role in total GHG budgets. Our meta-regression shows beaver wetlands (dam-builders only) to be worth approximately 75 million USD(2017) per year in GHG sequestration (Table 5; variable GHG).

Water purification

Beaver wetlands act as buffer zones by filtering compounds and human-caused pollutants (heavy metals, disease-causing agents, nitrogen), thus increasing water quality and lessening the costs of downstream wastewater treatment (Skinner et al. 1984, Smith et al. 1991). Filtration in general is a highly beneficial service to societies, and the purifying action of beaver dams (dam-builders only) is worth approximately 28 million USD(2017) per year (Table 5; variable Quality). Savings from natural water filtration services are often compared to the value of investments needed for manual water filtration, as conserving natural wetlands or building artificial ones may decrease the costs incurred to water filtration plants by purifying water prior to it passing through the plant. When quantifying the purification ability of one km^2 of beaver wetland (80000 m^3) in Balodis (1994) with values from Whitfield et al. (2015), beavers (dam-builders only) may aid in purifying ca. 0.8 billion m^3 of water per year.

Provisioning services provided by beavers

Water supply

Water regulation by beaver dams raises groundwater levels both upstream and downstream of the dam. Increases in groundwater storage capacity, water table level, and aquifer recharge have been observed in several studies (e.g. Westbrook et al. 2006, Grygoruk & Nowak 2014). Grygoruk and Nowak (2014) estimated the annual water storage value provided by beavers in Krzemianka Valley, Poland, to approximately equal € 4000. In our meta-regression results, the water supply service totalled 20 million USD(2017) per year (dam-builders only; Table 5; variable Supply).

Recreational hunting and fishing

Extractive goods from beavers include food, materials (castoreum for the perfume industry and pelts), and medicinal resources (castoreum for the natural products industry). Annual harvest levels vary between 1 and 5% in North America, 12% in Europe, and 2% in Russia, which equates to approximately 580000 beavers killed annually in total (Belova et al. 2015, White et al. 2015, Florek et al. 2017, Borisov & Baranov 2018). The large harvest percentage in Europe is influenced by numbers killed in Finland, where North American beavers occur as an invasive species close to, and in certain areas sympatrically with, European beavers (Parker et al. 2012, Alakoski et al. 2019). The lack of accurate hunting data from Russia may well explain the small percentage there; Russian hunting statistics underestimate actual annual hunting levels, meaning that extractive beaver goods are actually more valuable than our calculations show. Hunting cultures in each of the Northern Hemisphere areas may value different aspects in beaver hunting (meat, pelts, castoreum), and openly accessible information is not available for the percentage of castoreum and beaver meat entering consumer markets in relation to total hunting levels. It is important to remember that products still have value even if they do not enter consumer markets, as hunters can utilise the meat, pelts, and castoreum themselves. Beaver-created wetlands also offer raw material and food output services in the form of improved hunting and fishing opportunities, due to increasing game (e.g. waterfowl, Nummi & Holopainen 2014) and fish (e.g. Schlosser & Kallemeyn 2000) populations occupying these wetlands. Recreational hunting and fishing in beaver wetlands (dam-builders only) is worth 1.6 million USD(2017) per year (Table 5; variable HuntFish).

Supporting services provided by beavers

Habitat and biodiversity provision

Biodiversity as a service is important to human societies because it upholds and regulates ecosystem functioning, stability, resilience, productivity, and nutrient dynamics (Mace et al. 2012, Clark et al. 2014). Decreasing biodiversity diminishes the capability of ecosystems to uphold the services they provide to human society.

Wetlands are important hot spots for species diversity, and as they are globally becoming increasingly rare habitats, the beaver provides habitat and biodiversity provision ecosystem services by aiding in their creation and by increasing habitat heterogeneity (Wright et al. 2002, Hyvönen & Nummi 2008, Nummi & Kuuluvainen 2013, Willby et al. 2018).

An estimated 195000–260000 km^2 of wetlands in the USA have been converted to agriculture and other land-use types during 1835–2000 (Baker & Hill 2003). Whitfield et al. (2015) estimate that, since 2000, beavers have globally created 9500–42000 km^2 of new wetlands, meaning that, since then, global beaver wetlands have compensated for 5–16% of United States wetland loss. A meta-analysis by Stringer and Gaywood (2016) shows the overall positive influence of beavers on biodiversity despite a few negative effects on, e.g., caddisflies (Trichoptera) through decreased lotic conditions, and lamprey (*Lampetra* spp.) and Atlantic salmon (*Salmo salar*) through impeded mobility due to dams.

Beavers may facilitate the rehabilitation and restoration of freshwater habitats in a cost-effective manner (Gorshkov et al. 1999, Kemp et al. 2012). Populations of several aquatic invertebrates, fish, amphibians, waders, ducks, and bats increase in beaver-created habitats (Rosell et al. 2005, Stringer & Gaywood 2016 and references therein), and even entire communities of certain species groups may benefit (Nummi & Holopainen 2014). Beaver wetlands (dam-builders only) contribute ca. 133 million USD(2017) per year to habitat and biodiversity services (Table 5; variable HabBio).

Other nutrient cycling

Gren (1995) suggests that the abatement capacity of a hectare of natural wetlands ranges from 100 to 500 kg nitrogen per year. Several studies have observed beaver ponds to cause reductions in total nitrogen, total phosphorus, and dissolved silicate levels (e.g. by 18, 21, and 32%, respectively; Correll et al. 2000). A beaver dam can withhold 9–6355 m^3 of sediment during its life-span (Nummi et al. 2018), which means that current active dams could hold between 7 million and 9 billion m^3 of sediments during their lifetimes (assuming one pond per colony, 895000–1.5 million dam-building colonies in Table 2). Nutrients are also retained upstream through sediment detainment (Naiman et al. 1994), potentially improving soil quality. This, coupled with increased over-bank flooding, provides an important nutrient boost in upstream floodplains (Wohl 2013). Beaver wetlands (dam-builders only) may store 1–7.5 billion kg nitrogen per year when calculated using figures from Gren (1995). We did not find value estimates for the maintenance of soil fertility during our literature search, which is why our meta-analytical function transfer does not include this ecosystem service.

Cultural services provided by beavers

Non-consumptive recreation

Beavers generate habitats suitable for recreation and relaxation, providing, e.g., canoeing and bird-watching possibilities. Generating habitats for recreation may be regarded as a cultural service for recreationists, which not only provides monetary value to societies but also produces mental and physical well-being. In the Northern Hemisphere, recreation in beaver wetlands (dam-builders only) could be worth 43 million USD (2017) per year (Table 5; variable Recreation).

DISCUSSION

We have comprehensively utilised all available knowledge to aggregate information on beaver activity for the Northern Hemisphere, which, to our knowledge, has not been done before. None of the ecosystem services included in our meta-analytical function transfer proved significant in the calculations, but this only shows that all wetland services in the Northern Hemisphere are valued highly, rather than one or two services being particularly prized. By scaling up the meta-regression coefficients, we show that beavers provide valuable ecosystem services, ranging in value from ca. 1.6 million (recreational hunting and fishing; variable HuntFish) to 133 million (habitat and biodiversity provision; variable HabBio) USD(2017) per year over the whole Northern Hemisphere. The meta-analytical function transfer offers municipality planners and wildlife managers the possibility of roughly estimating local beaver wetland services to aid in beaver management and wetland planning, and scaling up values provides decision-makers with new information that may be incorporated into water management and conservation, such as implementation of the European Union's Water Framework Directive.

In absolute terms, habitat and biodiversity services in beaver wetlands proved to be the most valuable in our analyses, although non-consumptive recreation produced the highest annual per-hectare value. Habitat and biodiversity services benefit society through riparian zone restoration by beavers and increased climate change adaptation caused by increased ecological resilience. Non-consumptive recreation was valued third highest over the whole area. However, our valuation is based on general freshwater mineral soil wetlands located between the northern and southern latitude limits (69°N and 26°N) of beaver range in the Northern Hemisphere rather than on specific beaver wetlands, and the distinction may be especially apparent with non-consumptive recreation services. Northern Hemisphere wetlands are considered very important in terms of recreation due to their limited availability (as vast wetland areas have been lost) and high utilisation level. Beaver wetlands, a specific subtype of Northern Hemisphere wetlands, potentially offer less than average recreation services due to their distinct characteristics, i.e. small size, access difficulties and a tendency to become overgrown with vegetation and change in habitat characteristics. Although some recreational sites have been set up specifically to showcase beaver activity and encourage beaver-related nature tourism (e.g. in Scotland, Finland), these generate little income compared with our valuation results. So, despite our efforts to ensure that our meta-regression would not overestimate ecosystem service values, non-consumptive values may indeed be exaggerated.

Several services mitigate the harmful effects of climate change to society, which are projected to worsen in the coming decades. Greenhouse gas sequestration proved to have the second lowest annual per-hectare value, but as the service is not restricted to area or human density it was ascertained to be the second highest in value in absolute terms. How GHG dynamics behave in beaver impoundments is still largely unknown, due to great fluctuations and spatiotemporal variation. The role of GHG sinks and emissions in the ecosystem services concept is concurrently a double-edged sword. While GHG sinks benefit humans in terms of climate change mitigation, it is easy to think that GHG emissions automatically function in an opposite manner. However, GHG dynamics are a natural part of wetland functioning, and therefore, even emissions from beaver wetlands may be seen as ecosystem services. These natural emissions uphold the structure of wetland ecosystems, thereby indirectly creating, e.g., habitat and biodiversity services at local scales. On the other hand, from a global perspective, all GHG emissions, irrespective of whether they are natural or anthropogenic, contribute to climate change, and are therefore disservices. Our meta-analysis only included mineral soil ecosystem service valuations, while beaver activity obviously influences peatland areas as well. Moderation of extreme events and water purification also play a part in alleviating the effects of climate change. Moderation of extreme events proved the third most beneficial in annual per-hectare values, while being fourth most valuable in absolute terms. Increased sediment deposition in beaver wetlands lessens the harmful effects of erosion (Pollock et al. 2017), and periodic overbank flooding upholds hydrological and ecosystem processes in floodplain areas, benefitting, e.g., agriculture (Westbrook et al. 2006), but we were unable to calculate a value for nutrient cycling.

Beaver range is expanding in Europe, and several countries are realising the potential of utilising beaver activity for water management (Törnblom et al. 2011, Kaczyński 2014), wetland restoration (Pollock et al. 2017), and climate change mitigation (Baldwin 2017). Increasing beaver populations bring with them growing benefits and disadvantages; these must be balanced to ensure successful reintroductions and wetland restoration along with social acceptance. Societal utilisation should be maximised, while minimising damage.

Ecosystem services and disservices are scale-dependent. Upholding wetland health and productivity is a public concern, yet the Northern Hemisphere also has significant private ownership of wetlands. Most services provided by beavers and wetlands are free to be enjoyed by society as captured value, often invisibly. On the other hand, costs, i.e. external value, are often accrued to a small group of individuals, who sometimes endure repeated disservices. Beaver activity is also area-dependent, which is why the magnitude of each ecosystem service and disservice provided varies from wetland to wetland and between individuals benefitting or incurring losses. Existing literature and knowledge concerning the ratios of beaver habitats are deficient, and producing more accurate information on this would help in assessing how various beaver habitats influence the provision of ecosystem services. Beaver management has long been focused on single disservices and how to prevent or mitigate them. When broadening the analysis from individual disservices to landscape-level effects, the number of stakeholders and their interests naturally increases manyfold. Future active beaver management should incorporate a broader horizon, including not only small-scale hindrances, but also a wider paradigm shift towards considering landscape-level and societal effects as well.

The greatest positive outcomes are to be gained when disservices are constrained while concurrently supporting and promoting service provisioning. Tools are needed to ensure landowners gain more than they lose from beaver conservation. Including numerous stakeholder opinions is obviously a complex procedure, but it is possible, if, e.g., Payment for Ecosystem Services schemes are introduced. This could enable stakeholders downstream of a dam or flood zone to compensate landowners at the flood site for benefits gained downstream, while simultaneously offsetting any damages accrued to landowners.

Our study has several limitations. First, our calculations are conditional on how accurate the values are that we have found from the literature. To control the resulting uncertainty, we have used the minimum and maximum values mentioned in the literature and, in the case of beaver population size, we only used the minimum estimate for North American beavers. We also limited our value estimate calculations to dam-building beavers only, i.e. to 50% of the Northern Hemisphere beaver population. These actions help prevent gross overestimations and ensure that our calculations remain conservative. Uncertainty in beaver population sizes also limits our study, as the most recent official estimates for the North American population are several years old. However, this does not affect our per-hectare value estimates, which can be used for estimating the value of individual sites. Meta-analytical value transfer is a method for scaling theoretical values for beaver sites with known areas or populations. Our hemisphere-wide valuations can also be recalculated in the future when more accurate population estimates become available.

Second, as no prior work exists on specifically valuing the ecosystem services of beaver activity, no valuation studies existed for our meta-analytical value transfer. We therefore used studies valuing the ecosystem services provided by freshwater mineral soil wetlands located between the northern and southern latitude limits (69°N and 26°N) of the Northern Hemisphere beaver range, which are used to represent beaver habitats. Meta-analytical function transfer is a method specifically designed for valuing services over large areas. The method has previously been used for a similar purpose, e.g. to estimate global wetland value (Woodward & Wui 2001), yet it has limitations in accuracy and consistency. However, to minimise issues with this, we adjusted values from various contexts, e.g. price and income levels, currency data, site area, and study year, into analogous units. Also, to avoid any potential issues with double counting, we did not aggregate all ecosystem service values into one total value.

Third, we were only able to utilise English-language sources in our value transfer, meaning that we may have missed some texts valuing local wetland ecosystem services. Fourth, we were unable to quantify the value of beaver activity in terms of nutrient cycling or historical value, as none of the documents in our meta-analytical function transfer included estimates on these particular ecosystem services. Fifth, our results may show aggregation bias, which prevents the statistical analyses from uncovering significant differences between the explanatory variables. However, we do not consider this to be a large problem, as the wider idea of our study is to help managers and decision-makers recognise and even determine the approximate values of individual beaver sites. Sites are highly variable, so they are not identical in which services they provide and to what degree. Our per-hectare values are therefore useful for estimating how much an area may be worth in terms of predetermined ecosystem services, and for comparing benefits with potential disservices.

CONCLUSIONS

Understanding how the economic impacts of beaver activity function and are defined is imperative for improving the future management of beaver populations. Until now, no attempts have been made to quantify the positive effects of beaver activity in one study. Our aim was to expand on and consolidate previous research to gain a large-scale perception of the value of beaver activity, and also to produce value estimates that future researchers may use for estimating the economic value of individual beaver sites or sites in larger geographic areas. The importance of and need for all-encompassing management and planning may very well expand in the future, as beaver populations continue growing in Eurasia, and individuals and colonies spread into increasingly urban areas and human habitation persistently encroaches on beaver habitat.

This study is a first attempt at gaining an idea of ecosystem services provided by beavers. We show that habitat and biodiversity, non-consumptive recreation, and moderation of extreme events are particularly valuable services. Though the North American beaver population is currently stable, the Eurasian beaver population is increasing, which will lead to increasing benefits and disadvantages from beaver activity. These must be balanced to ensure social acceptance of the species and to maximise social welfare while damage is minimised. In a future of increasing climatic uncertainty, beavers may play a notable role in stabilising hydrological conditions. Implementing Payment for Ecosystem Services schemes to utilise the positive aspects of beaver activity is possible and offers a concrete way for societies to benefit while mitigating the economic losses accrued to landowners. However, questions remain, particularly concerning the biogeochemical effects of beaver wetlands. Currently, the scientific research community has no clear picture of how beavers affect GHG dynamics. More studies should be conducted on how the trade-offs between GHG emissions and sequestration function. Markets exist for these ecosystem services (Ezzine-de-Blas et al. 2016), and understanding how these services behave in beaver wetlands is an important next step.

ACKNOWLEDGEMENTS

This study was funded by the Kone Foundation, the Maj and Tor Nessling Foundation, and the Emil Aaltonen Foundation. We sincerely thank Niko Kulha (Finnish Environment Institute) and Matti Mäntynen (Metsähallitus) for assistance with the geographic information system analyses.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Ecosystem service valuation sources used for the literature review.

Appendix S2. Primary valuation studies used in the meta-analytical function transfer.