Large herbivores and aquatic–terrestrial links in southern boreal forests

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Summary

1. Concurrent measurement of population dynamics and associated spatio-temporal patterns of resource flow across aquatic–terrestrial boundaries are rare, yet necessary to understand the consequences of cross-habitat resource flux. Long-term study of the moose *Alces alces* (L.) population in Isle Royale National Park (Lake Superior, USA) provides an opportunity to examine the patterns of resource flux from aquatic to terrestrial habitats over ~50 years.

2. We analysed the spatio-temporal dynamics of aquatic-derived nitrogen (N) that moose transfer to terrestrial systems by using excretion models, foraging parameters, moose densities, and moose carcass locations ($n = 3616$) collected from 1958–2005.

3. Results suggest that moose transfer significant amounts of aquatic-derived N to terrestrial systems, which likely increases terrestrial N availability in riparian zones. A seasonal increase in terrestrial N availability when moose are foraging on N-rich aquatic macrophytes would contrast with the depression of soil N mineralization previously attributed indirectly to moose.

4. Aquatic foraging by moose and moose carcass locations are significantly clustered at multiple scales, indicating that grey wolves *Canis lupus* (L.) and moose can create concentrated areas of resource transfer due to clustered predation and foraging patterns.

5. This study shows that patterns of faunal-mediated resource transfer can depend significantly on predator–prey dynamics, and that large predators in this system influence herbivore-controlled resource transfer between ecosystems. Given the circumpolar extent of moose, they constitute an important, unquantified aquatic–terrestrial resource vector in boreal systems.

Key-words: predator–prey, resource flow, riparian, susbsidies, trophic cascade

Introduction

Resource flux across habitat boundaries affects species interactions and the stability of ecosystems (Likens & Bormann 1974; Huxel & McCann 1998; Loreau & Holt 2004; Polis, Power, & Huxel 2004; McCann, Rasmussen, & Umbanhowar 2005), primary productivity (Odum, Finn, & Franz 1979; Polis, Anderson, & Holt 1997), and biological diversity patterns (Moore *et al*. 2004; Croll *et al*. 2005). Flux between habitats depends on adjoining physical characteristics and biological vectors. The specific physiology and behaviour of a biotic vector can significantly influence the patterns and consequences of a resource flux (e.g., Ben-David *et al*. 2005). For example, faunal-mediated nutrient and energy fluxes are important between marine and terrestrial systems via salmon,

birds, and river otters (Naiman *et al*. 2002; Ben-David *et al*. 2005; Croll *et al*. 2005), and between rivers or lakes to riparian zones via emerging aquatic insects (Sabo & Power 2002a; Knight *et al*. 2005). Long-term, measurement of population dynamics and associated spatio-temporal patterns of resource flow across aquatic–terrestrial boundaries are rare (reviewed in Polis *et al*. 2004; Ballinger and Lake 2006; but see Ben-David *et al*. 2005 for an exception). Here we examine multi-decadal patterns of resource flow from aquatic to terrestrial habitats via moose in Isle Royale National Park (544 km^2 archipelago in Lake Superior, USA; 48°N, 89°W).

Moose are aquatic–terrestrial interface specialists (*sensu* Ballinger and Lake 2006), foraging extensively on aquatic macrophytes during spring and summer (Franzmann & Schwartz 1997), and excreting and dieing most frequently in terrestrial habitats (Franzmann & Schwartz 1997; Peterson 1977). Hence, moose comprise an unquantified vector for the

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transport of aquatic materials into terrestrial systems and a resource loss pathway for aquatic ecosystems. Aquatic resources ingested by moose are either deposited as urine and faeces or are incorporated into moose biomass. Significant soil and terrestrial plant responses to urine and faecal returns are well quantified for large herbivores (McNaughton 1985; Hobbs 1996; Frank 1998; Olofsson, Stark, & Oksanen 2004), including moose on Isle Royale (Pastor *et al.* 1993). Large herbivores are typically considered a resource for secondary consumers (e.g., Wilmers *et al.* 2003), but can also directly contribute to detritivore and producer communities (Danell, Berteaux, & Brathen 2002; Carter, Yellowlees, & Tibbett 2007). Consequently, aquatic-derived resources can flow through either moose excretion or biomass pathways and enter consumer, producer, or detritivore communities.

Boreal forests are well suited for examining spatial patterns of resource flow across aquatic–terrestrial boundaries. The boreal forest is a large circumpolar biome and covers ~28% of the North American continent north of Mexico (Larsen 1980). Moose are the largest member of the deer family (Cervidae), and their distribution parallels that of the boreal forest (Franzmann & Schwartz 1997). Adult moose carcasses represent substantial (270–550 kg), highly concentrated pools of labile nutrients available to predators (e.g., grey wolves), scavengers (Wilmers *et al.* 2003), and detritivore communities (Carter *et al.* 2007). Generally, boreal soils are relatively young (< 10 000 year.), nutrient-poor spodosols (Larsen 1980). Above-ground net primary productivity in boreal forests is typically 380 g m^{-2} year^{-1} (Saugier, Roy, & Mooney 2001). Lentic systems in boreal regions exhibit more variable annual productivity, ranging from 300 g m^{-2} year^{-1} to as low as 5 g m^{-2} year^{-1} (Wetzel 2001). This forest–aquatic comparison is important because the ecological significance of resource flux is thought to be positively related to asymmetrical productivity between ecosystems (Polis *et al.* 1997). Hence, the variability in productivity of boreal aquatic systems and the ubiquitous presence of a proficient resource vector via moose, emphasize the importance of understanding the dynamics of aquatic–terrestrial resource transfer for this biome.

We investigated the quantity and spatio-temporal patterns of nitrogen (N) flux via moose from aquatic to terrestrial habitats of the Isle Royale ecosystem. Nitrogen was the focus because this element is usually the most limiting in temperate and boreal forests (Larsen 1980). Daily and annual aquatic to terrestrial N flux was quantified based on excretion models and forage N analysis. Spatio-temporal patterns of the moose-mediated flux were quantified based on long-term (1958–2005) moose population estimates, carcass site clustering, and the areal extent of aquatic-derived N dispersion in the terrestrial system versus removal in aquatic systems. These analyses help answer questions such as: is the aquatic to terrestrial N flux via moose ecologically significant? What are the effects of moose in southern boreal forests and aquatic ecosystems? How are resource flux patterns related to predator–prey population dynamics? What is the ecological consequence of moose population restoration or extirpation?

Methods

AQUATIC TO TERRESTRIAL NITROGEN FLUX VIA MOOSE EXCRETION

We partitioned excretory nitrogen (N) returns of aquatic origin from biomass returns because these distinct resource pathways operate on separate time-scales. Excretion occurs daily whereas mortality due to predation or starvation is relatively pulsed. Estimation of daily excretory N flux from aquatic to terrestrial habitats via moose was based on N excretion models developed by Hobbs (1996; 2006). The total daily N added to an environment through ungulate urinary and faecal excretion can be expressed as a function of body mass and plant N content (Hobbs 2006). Total daily excretory N (N_t, g day^{-1} individual^{-1}) returned to the system per moose is expressed as,

$$N_t = F_p + U_p + F_e + U_e \qquad \text{eqn 1}$$

where F_p, U_p, F_e, U_e, represent faecal N of plant origin, urinary N of plant origin, endogenous faecal N, and endogenous urinary N respectively, as defined by Hobbs (2006; Appendix S1). These excretory models were empirically developed for elk diets in Colorado, USA (Hobbs 2006). For southern boreal forests, we used a range of moose summer intake rates (2·6–3·5 % of body mass per day in dry matter; p. 450 in Franzmann & Schwartz 1997) and plant N content reported for summer terrestrial and aquatic forage on Isle Royale (0·72–3·66% dry matter; Tischler 2004). Body mass used was the whole weight mean (408·25 kg) for cows ($n = 2$) and bulls ($n = 3$) measured for Isle Royale moose in winter (Peterson 1977).

The proportion of N_t (equation 1) that was of aquatic origin, 0·14–0·37, was determined using recent estimates of the aquatic fraction of summer moose diets based on stable carbon and nitrogen isotope analyses (Tischler 2004). The range in aquatic diet fraction is comparable to a previous estimate of 0·18 (Belovsky & Jordan 1978). Consequently, if A indicates the aquatic diet fraction range, then N of aquatic origin ($N_{aquatic}$ g day^{-1} individual^{-1}) excreted when moose are feeding on aquatic macrophytes is estimated by,

$$N_{aquatic} = N_t \times A \qquad \text{eqn 2}$$

$N_{aquatic}$ (equation 2) constitutes an ecologically meaningful estimate of the daily N individual moose transfer from aquatic to terrestrial systems. This estimate assumes moose excretory returns directly to aquatic systems are negligible, which is initially reasonable given that aquatic feeding bouts average 42·8 min day^{-1} on Isle Royale, digestive retention times typically exceed 12 h, and moose in summer spend about 5× more time per day on land than foraging in aquatic habitats (Belovsky & Jordan 1978). In 65 h of viewing moose foraging in water shallow enough to permit proper detection, defecation was never observed, while in 48 h of terrestrial observation, defecation was frequently observed (Belovsky & Jordan 1978). In calculating $N_{aquatic}$, intake rate was held constant at the median summer intake value reported for moose (3·1% of body mass per day in dry matter; Franzmann & Schwartz 1997).

Terrestrial nutrient fluxes are informative and comparable when carried out on a per unit area per year basis (Hobbs 2006). Therefore, per unit area total summer excretory N additions of aquatic origin (N_{flux} kg ha^{-1} year^{-1}) for moose densities found in North America (0–10 individuals km^{-2}; Franzmann & Schwartz 1997) were estimated as,

$$N_{flux} = (N_{aquatic} \times P \times D) \div S \qquad \text{eqn 3}$$

where P is moose population density, D is the number of days aquatic foraging typically occurs on Isle Royale (we used 108 days; Belovsky & Jordan 1978) and S the mean summer core-area size (0·4 km^2; Dussault *et al.* 2005).

The relative importance of N_{flux} was explored by comparison to annual terrestrial N cycling components: net N mineralization [20 kg ha^{-1} year^{-1} measured in three forests by Pastor *et al.* (1993) on Isle Royale], dissolved inorganic N runoff [1·6 kg N ha^{-1} year^{-1} reported maximum for boreal forests (Wetzel 2001)], and atmospheric deposition [3 kg N ha^{-1} year^{-1} reported for Isle Royale (Stottlemyer, Travis, & Toczydlowski 1995)]. N_{flux} was expressed as a percentage of these terrestrial N cycling components.

LONG-TERM FLUX DYNAMICS

Total annual N flux from aquatic to terrestrial habitats via moose on Isle Royale for 1915–2005 was calculated using a modified N_{flux} (equation 3) expression. Annual adult and yearling moose population estimates replaced moose population density (P). Methods for annual moose censuses since 1958 have been reported elsewhere (Vucetich & Peterson 2004). Moose population estimates before 1958 are less reliable and are included to illustrate general trends only (Peterson 1977). The mean summer core-area size (S) was replaced by an ecologically meaningful estimate of the maximum spatial extent that aquatic-derived resources are distributed over the terrestrial landscape via moose. This terrestrial N dispersion estimate was the core-area radius multiplied by total length of inland lake shoreline available for moose foraging [i.e., 276 km × 0·36 km = ~100 km^2 (10 000 ha)].

SPATIAL DYNAMICS OF AQUATIC TO TERRESTRIAL RESOURCE FLUX VIA MOOSE

Theory indicates that spatial subsidies can substantially influence community structure by affecting rates of local competition for producers and consumers (Holt 2004; Loreau & Holt 2004). The location at which aquatic-derived resources that are incorporated into moose biomass enter producer, consumer, and detritivore pathways was analysed using moose carcass locations collected from 1958–2005 ($n = 3616$). Carcass locations were determined in winter during aerial surveys, with subsequent ground inspection, and in spring and summer through extensive, island-wide hiking (Peterson 1977; Vucetich & Peterson 2004). The number of carcasses within a 1-km radius was calculated for each carcass location. High- and low-density carcass clustering was analysed using global and local indicators of spatial association (i.e., Getis-Ord general G, local Getis-Ord Gi* and Local Moran's I, Fortin and Dale 2006). The Getis-Ord general statistic summarizes spatial autocorrelation for the entire study area, while the local Getis-Ord Gi* and Local Moran's I statistics assess autocorrelation within the 'neighbourhood' of locations within a 1-km search radius. Hence, the global spatial statistics permit summarizing the spatial pattern over the entire island and the local statistics identify areas of density relatedness and significant clustering at the 1-km scale, i.e. 'hot and cold spots' (Anselin 1995; Fortin and Dale 2006). These statistics help answer questions such as, do areas of high or low carcass density tend to cluster on the landscape, and does clustering occur at multiple scales? Euclidian distance and inverse distance squared methods were used in the clustering analysis.

Water depth typically limits moose foraging in aquatic habitats to near-shore, littoral zones (Franzmann & Schwartz 1997). In contrast, physical features do not generally limit where moose forage in terrestrial

habitats and mortality can occur anywhere on the landscape. Consequently, we expected that the areal extent of the donor system resource shadow (i.e., a zone from which energy, materials, or organisms have been diverted; the zone of aquatic plant removal in this study; *sensu* Polis *et al.* 2004) should be less than the extent of resource dispersion in the recipient, terrestrial system. The total resource shadow was estimated by dividing the range of daily aquatic forage consumption by an average of aquatic forage consumption per square metre reported for Isle Royale moose (Belovsky & Jordan 1978; Qvarnemark and Sheldon 2004), i.e. (0·655–1·081 kg dry matter day^{-1} moose^{-1}) ÷ (0·073 kg dry matter day^{-1} m^2 moose^{-1}). The quotient, 9–15 m^2 day^{-1} moose^{-1}, was then scaled to seasonal and population levels by multiplication by the number of days that moose forage on aquatic plants [i.e. D in equation (3); 108] and annual moose population estimates to yield approximations of the aquatic resource shadow each year. The comparative areal extent of aquatic resource transfer through excretion in the recipient terrestrial systems was estimated using the mean summer core-area size radius multiplied by total length of inland lake shoreline available for moose foraging [i.e., 276 km × 0·36 km = ~100 km^2 (10 000 ha)].

Results

AQUATIC TO TERRESTRIAL NITROGEN FLUX VIA MOOSE EXCRETION

The summer total daily N (N_t) excreted by Isle Royale moose increases as intake rate and forage N concentration rise, with a mean (± 1SD) on Isle Royale of 283 ± 37 g N day^{-1} moose^{-1} (Fig. 1a). N_t is more strongly influenced by plant N concentration than intake rate because urinary N excretion increases quadratically with forage N concentrations (Hobbs 1996; 2006). Similarly, the summer daily N of aquatic origin ($N_{aquatic}$) excreted by moose increases as the aquatic diet fraction and forage N concentration rise, with a mean (± SD) on Isle Royale of 78 ± 12 g N day^{-1} moose^{-1} (average of open plot section in Fig. 1b). $N_{aquatic}$ is more strongly influenced by plant N concentration than the aquatic diet fraction (note greater slope along z-axis compared to x-axis in Fig. 1a and b). The aquatic diet fraction range used (i.e., A in equation (2) = 0·14–0·37) in calculating $N_{aquatic}$ is conservative because the 95% CI reported by Tischler (2004) for this range is 0·09–0·57. Hence, $N_{aquatic}$ could be substantially lower or higher for individual moose. The total summer excretory N of aquatic origin (N_{flux}) transferred to terrestrial systems via moose on Isle Royale was (mean ± SD) 1·2 ± 0·2 kg N ha^{-1} year^{-1}, constituting 6, 75%, and 40% of net annual N mineralization, annual N runoff, and annual atmospheric N deposition, respectively (Fig. 2). At high moose densities, which often occur in riparian habitats relative to inland habitats during spring and summer (Peterson 1977), N_{flux} may be ~3× higher (Fig. 2).

LONG-TERM FLUX DYNAMICS ON ISLE ROYALE

Over the past century, terrestrial N gain via moose has exhibited 10-fold fluctuations, respectively, before and after wolf establishment (Fig. 3). Mean (± SD) annual N gain for riparian habitats for 1958–2005 was 1·06 ± 0·4 kg N ha^{-1} year^{-1}.
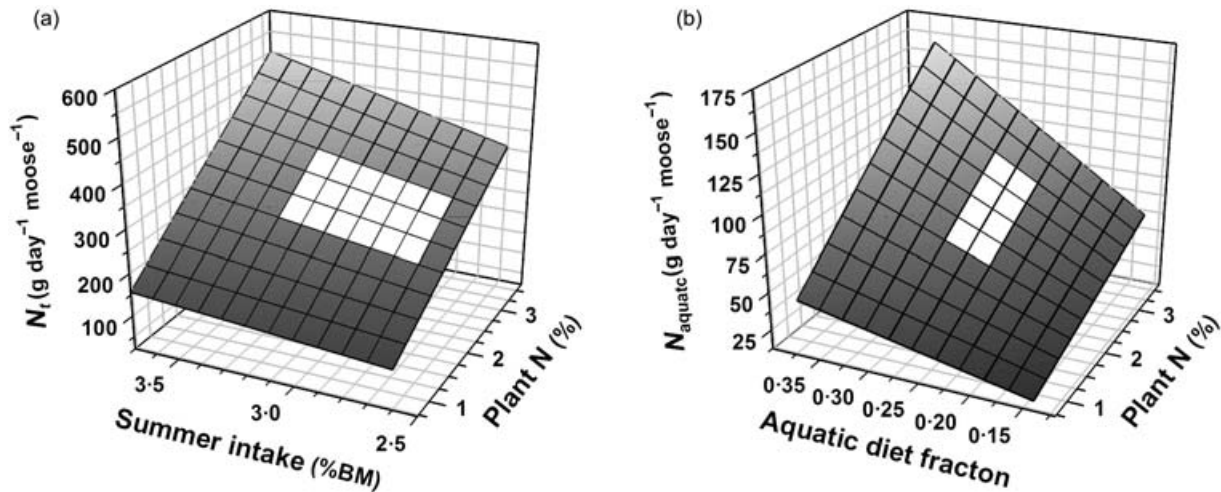
Fig. 1. Nitrogen excretion by moose (*Alces alces*). Open plot sections indicate best estimates for Isle Royale moose based on mean ± 1SD of model parameters. (a) Summer total daily nitrogen (N_t) excreted as a function of summer intake rate and the plant nitrogen concentration range exhibited for summer terrestrial and aquatic forage. (b) Summer da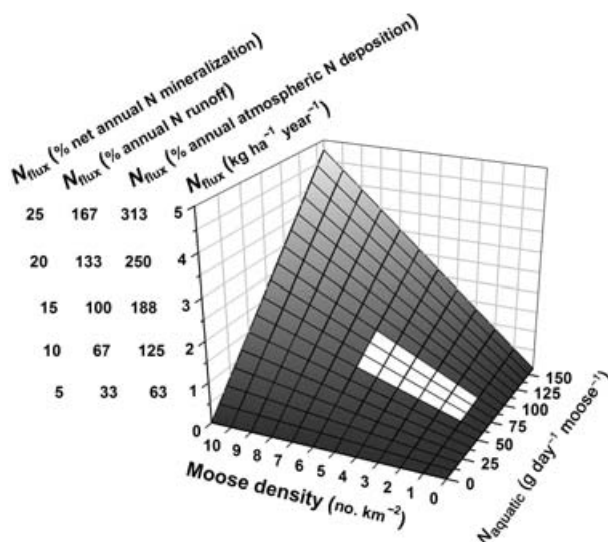ily nitrogen of aquatic origin ($N_{aquatic}$) excreted as a function of the summer aquatic diet fraction and the plant nitrogen concentration range exhibited for summer terrestrial and aquatic forage.

Fig. 2. Total summer excretory nitrogen of aquatic origin (N_{flux}) transferred to terrestrial systems via moose (*Alces alces*) as a function of North American moose population densities and the summer daily nitrogen of aquatic origin ($N_{aquatic}$) excreted by moose. Open plot section indicates best estimate for Isle Royale moose based on mean ± 1SD of model parameters. Additional *y*-axes indicate relative importance by expressing N_{flux} as a percentage of annual net nitrogen mineralization, annual forest runoff, and annual atmospheric deposition. See methods for values of these nitrogen cycling components used for comparison.

SPATIAL DYNAMICS OF AQUATIC TO TERRESTRIAL RESOURCE FLUX VIA MOOSE

The distribution of moose carcasses showed a striking degree of clustering at the island scale, with less than a 0·1% likelihood that the clustering of wolf-killed moose carcass sites resulted from random chance (Fig. 4b; Getis-Ord Gi z-score = 4·13 standard deviations; Getis and Ord 1992). Terrestrial dispersion

of aquatic-derived excretory resources transferred via moose is likely highest in riparian zones and within ~0·5 km of lake shorelines (Fig. 4b). The mean (± SD) extent of seasonal aquatic resource shadow (~1·2 ± km², range = 0·4–3·3 km²) was less than the scope of terrestrial distribution (~100 km²). However, the effects of littoral zone foraging by moose probably extend to pelagic zones, depending on lake mixing dynamics (Wetzel 2001).

Together, the Getis-Ord Gi* and Local Moran's I z-scores indicated that there was significant clustering of high-density and low-density carcass areas (Fig. 5a) and that sites of similar density were most often located adjacent to each other at local scales (Fig. 5b). The positively skewed z-score distributions (Fig. 5a) indicated that high-density ('hot spots') carcass sites were more strongly associated with one another than with low-density carcass sites ('cold spots'), and that similar carcass density values were more strongly associated (Fig. 5b).

Discussion

The relative importance of the moose-mediated N flux is dependent on terrestrial system net N mineralization. For example, Stottlemyer *et al*. (1995) found annual net N mineralization rates under dominant boreal tree species on Isle Royale to be below half of the rate used in this analysis (20 kg ha⁻¹ year⁻¹ from Pastor *et al*. 1993). Hence, N_{flux} could constitute at least double the percentage of net annual N mineralization and other N cycle components (Fig. 2). Comparing N_{flux} to other important N cycle components on Isle Royale (e.g., total plant uptake, alder and cyanobacteria N fixation, organic N availability) would, if data were available, refine our understanding of the relative importance of N_{flux}. However, our N_{flux} estimate (mean ± SD = 1·2 ± 0·2 kg N ha⁻¹ year⁻¹) is similar to N fixation inputs by mosses that are argued to be important to boreal forests elsewhere (Zackrisson *et al*. 2004).
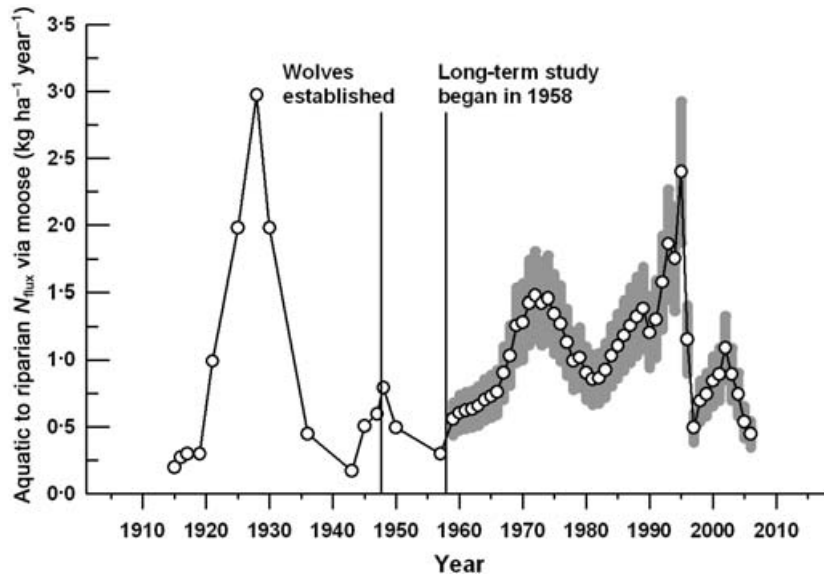
Fig. 3. Long-term excretory nitrogen of aquatic origin transferred to riparian zones via adult and yearling moose (*Alces alces*) on Isle Royale National Park (Lake Superior, USA). Shaded error bars since 1958 indicate 95% CI. Data before 1958 should be considered illustrative of a general trend only.

Variation in moose density is the most important determinant of total N_{flux} (Fig. 3) and largely subsumes the uncertainty associated with excretion and foraging parameters. Most North American moose population densities are > 1 moose km^{-2} (Franzmann & Schwartz 1997) and Isle Royale densities generally range ~1–6 individuals km^{-2} (Vucetich & Peterson 2004). However, N_{flux} could be substantially higher in areas where animals are concentrated in preferred foraging and resting sites. Over three individual moose per hectare have been recorded visiting Isle Royale mineral licks, all of which are near inland lakes (Risenhoover & Peterson 1986) and as many as nine different moose have been observed simultaneously foraging in an area less than 1 km^{-2}, on a single lake (Peterson 1995). Under such conditions, N transferred to terrestrial systems via moose could approach ~4·5 kg N ha^{-1} $year^{-1}$ in those areas, constituting much higher proportions of N cycling components (Fig. 2). Accordingly, the excretory N transferred from aquatic to terrestrial habitats via moose (Figs 1b, 2 and 4) likely increases terrestrial N availability within moose summer core areas. This suggestion contrasts with the depression of soil N mineralization previously attributed to feedbacks from moose foraging on Isle Royale (Pastor *et al*. 1993; Pastor, Cohen, & Hobbs 2006), but is supported theoretically.

Terrestrial ecosystems exhibit a dichotomous N cycling response to large mammal herbivory (reviewed in Pastor *et al*. 2006). Forage N concentrations are critical in determining nutrient accelerating or decelerating scenarios (*sensu* Ritchie, Tilman, & Knops 1998). This is based on observations that faecal N excretion increases linearly and urinary N excretion quadratically with forage N concentrations (Hobbs 1996; 2006). The resulting critical N concentration in forage is ~1·5% dry mass, above which mammalian herbivores excrete N primarily as urea to remove excesses, below which N is excreted primarily in faeces to maximize N retention (Pastor *et al* 2006). Urea-derived N is readily available to plants, but faecal N is less so and can lead to slower N mineralization

rates than found in soil humus alone (Pastor *et al*. 1993). Moose could seasonally increase terrestrial N cycling when foraging on N-rich aquatic macrophytes. The basis for this suggestion is the observation that two genera, *Potamogeton sp.* and *Myriophyllum sp.*, are readily consumed by moose and dominate shallow aquatic habitats on Isle Royale (Qvarnemark and Sheldon 2004). Mean N content of *Potamogeton sp.* (*n* = 28) and *Myriophyllum sp.* (*n* = 5) is 2·45% and 2·24% dry mass, respectively, compared to 1·3% for combined summer and winter terrestrial forage (*n* = 182; Tischler 2004). Aquatic foraging, therefore, would cause moose to excrete excess N primarily as urea in riparian zones and within ~0·5 km of lakeshores (Fig. 5b). It is important to note that the timing, duration, and intensity of aquatic foraging by moose is variable, ranging from the few months observed in our system to the year-round use of aquatic plants reported by Mac-Cracken, Vanballenberghe & Peek (1993) on the Copper River Delta, Alaska.

The effects of moose on the cycling of limiting nutrients in aquatic systems requires more scrutiny [(e.g. phosphorus (P)]. The significant influence consumers have on internal P cycling has been recognized (reviewed by Vanni 2002), but such analyses have not included moose. For example, turbation of lake sediments by moose while foraging for aquatic plants certainly releases P from interstitial sediment waters, where concentrations are orders of magnitude greater than in overlying water (Carpenter & Lodge 1993). Therefore, internal lake P supply rates could hypothetically increase, producing a net positive effect on lake P cycling despite the P loss due to moose herbivory. Testing such hypotheses is necessary to understand feedbacks between animal populations and ecosystem processes across ecological interfaces (Polis *et al*. 2004).

In this study, we did not quantify the fraction of aquatic forage incorporated into moose biomass. To do so is complicated by different assimilation efficiencies and availabilities of aquatic and terrestrial forages (Belovsky & Jordan 1978).
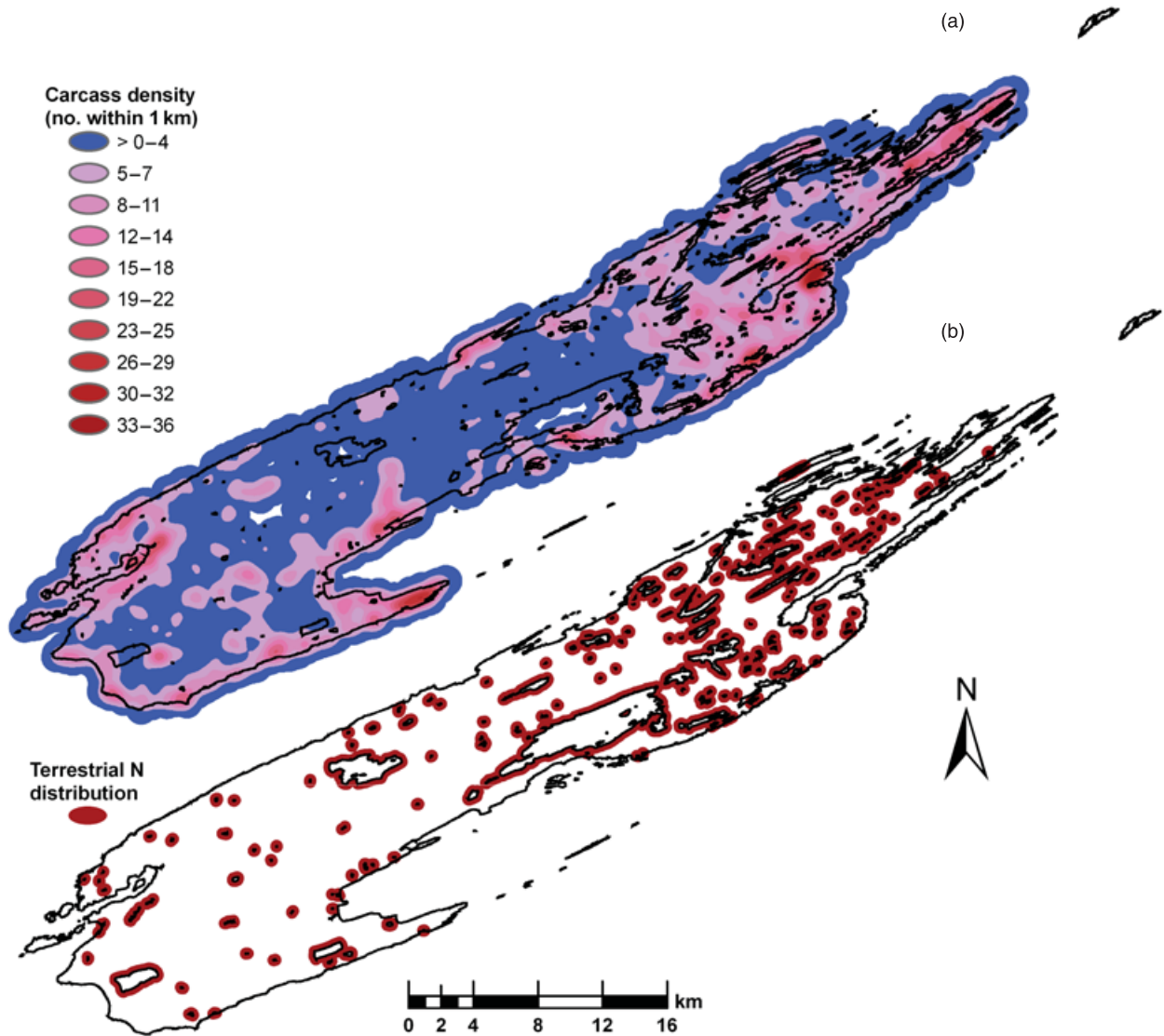
Fig. 4. Long term moose (*Alces alces*) carcass and aquatic–terrestrial resource flux distribution in Isle Royale National Park (Lake Superior, USA). (a) Moose carcass (*n* = 3616) density map 1958–2005. Island blank areas = 0 carcass density. (b) Aquatic-derived resource dispersion in the recipient terrestrial system. Buffer zone around interior lakes indicates probable mean summer core areas for moose foraging on aquatic macrophytes.

Fig. 5. Cumulative probabilities of local spatial statistic z-scores calculated for moose (*Alces alces*) carcass location densities (1958–2005; *n* = 3616) in Isle Royale National Park (Lake Superior, USA). Z-scores less than −1·96 or greater than 1·96 (i.e., one standard deviation) are considered significant at alpha = 0·05. Vertical reference lines mark one standard deviation. Horizontal reference lines mark where the probability functions intersect vertical reference lines. (a) Getis Ord Gi* z-scores indicate a third of carcass sites are located in areas of high (32%) or low (31%) carcass site density (i.e., hot or cold spots respectively). (b) Local Moran's I z-scores indicate 4% of carcass sites exhibit carcass densities dissimilar to adjacent areas, while about half (52%) of carcass sites are located in areas of similar carcass density.
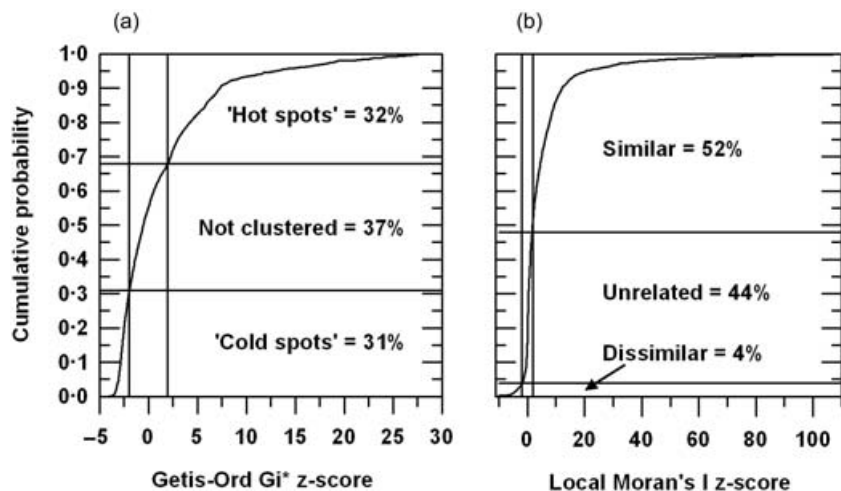
Even so, where moose consume aquatic vegetation, some fraction of moose biomass is undeniably aquatic in origin. Thus, moose link seasonal aquatic system productivity with terrestrial predator, scavenger, and detritivore communities. The analysis of long-term carcass patterns (Figs 4 and 5) indicates where such food web linkages occur on the landscape. Where such linkages occur is important to how aquatic subsidies affect feedbacks between above- and below-ground communities, competition, and the maintenance of ecosystem heterogeneity (Holt 2004; Loreau & Holt 2004; Polis *et al.* 2004). For example, Isle Royale moose carcasses, despite being very well utilized by wolves and scavengers, increase soil macronutrients and microbial biomass, shift soil microbial composition, and elevate leaf nitrogen for at least 2–3 years in plants at kill sites (Bump *et al.* in review). The moose carcass location pattern reveals that the transfer of aquatic subsidies via moose biomass to upper trophic levels and detritivore communities is clustered over time, at multiple scales (Fig. 4). Mechanisms influencing carcass 'hot' and 'cold' spots include island-scale habitat features and smaller-scale predation patterns.

Fire patterns and differential regeneration of balsam fir *Abies balsamea* (L.), an ecologically important winter-browse species, correlate with the typical island-wide spatial pattern in moose density. The highest moose densities (~5·4 individuals km^{-2}) are at the east end, low densities mid-island in major 1936 burn areas (~0·8 individuals km^{-2}), and moderate densities (~1·8–3·4 individuals km^{-2}) at the west end (Vucetich and Peterson 2004). The direct influence of wolves on the spatial distribution of carcasses, and thereby patterns in the moose-mediated resource flux, is readily observable. Wolves kill moose in some regions of the landscape at up to 12× the rate of other regions (Bump *et al.* in review). On Isle Royale, kills of calves are usually near shorelines, in heavy cover, while adult kills appear more randomly distributed (Peterson 1977; Stephens and Peterson 1984). In summer, cow moose and calves are significantly associated (~2× more likely than bulls) with human camp grounds (and no wolves), which are almost all situated on shorelines (Stephens and Peterson 1984). Moose densities in winter, which are important for assessing where aquatic resources incorporated into moose biomass are distributed, averaged 415% greater on small islets than on the main island (Stephens and Peterson 1984). Hence, moose habitat selection reflects trade-offs between acquiring essential resources and avoiding predators (Stephens and Peterson 1984; Dussault *et al.* 2005), which results in excretion and carcass spatial patterns (Fig. 5).

These results indicate that moose are an important aquatic–terrestrial resource vector in boreal systems, conferring a net N influx to terrestrial habitats from aquatic habitats. Future refinement of the first approximations made in this study may result in different modelling parameters and flux estimates, but such improvements will not likely alter the qualitative importance of our conclusions. Resource dispersion in the recipient system will typically be more extensive than the donor system resource shadow due to the landscape-level terrestrial range of moose and depth-restricted extent of their littoral zone foraging. Repeated use of specific areas and clustering of moose carcasses over time can create highly concentrated areas of resource transfer in recipient systems. The consequences of the resource flux estimated here require further study, especially the effects of moose on aquatic ecosystems: the direct net influence on water chemistry, lake sediment disturbance, and the potential indirect effects on aquatic food webs (i.e., phytoplankton, zooplankton, fish populations) are unresolved. Wolves influence moose populations, habitat use, and carcass distribution. Wolves, therefore, have a cascading impact on aquatic–terrestrial resource subsidies transferred via moose.

References

Anselin, L. (1995). Local indicators of spatial association – LISA. *Geographical Analysis*, **27**, 93–115.

Ballinger, A. & Lake, P.S. (2006). Energy and nutrient fluxes from rivers and streams into terrestrial food webs. *Marine and Freshwater Research*, **57**, 15–28.

Belovsky, G.E. & Jordan, P.A. (1978). Time-energy budgets of moose. *Journal of Theoretical Biology*, **14**, 76–104.

Ben-David, M., Blundell, G.M., Kern, J.W., Maier, J.A.K., Brown, E.D. & Jewett, S.C. (2005). Communication in river otters: creation of variable resource sheds for terrestrial ecosystems. *Ecology* **86**, 1331–1345.

Carpenter, S.R. & Lodge, D.M. (1993). Effects of submersed macrophytes on ecosystem properties *Aquatic Botany*, **26**, 341–370.

Carter, D.O., Yellowlees, D. & Tibbett, M. (2007) Cadaver decomposition in terrestrial ecosystems. *Naturwissenschaften*, **94**, 12–24.

Croll, D.A., Maron, J.L., Estes, J.A., Danner, E.M. & Byrd, G.V. (2005). Introduced predators transform subarctic islands from grassland to tundra. *Science*, **307**, 1959–1961.

Danell, K., Berteaux, D. & Brathen, K.A. (2002). Effect of muskox carcasses on nitrogen concentration in tundra vegetation. *Arctic*, **55**, 389–392.

Dussault, C., Ouellet, J.P., Courtois, R., Huot, J., Breton, L. & Jolicoeur, H. (2005). Linking moose habitat selection to limiting factors. *Ecography*, **28**, 619–628.

Fortin, M. & Dale, M.R.T. (2006). *Spatial Analysis: A Guide for Ecologists*. Cambridge University Press, Cambridge, UK.

Frank, D.A. (1998). Ungulate regulation of ecosystem processes in Yellowstone National Park: direct and feedback effects. *Wildlife Society Bulletin*, **26**, 410–418.

Franzmann, A.W. & Schwartz, C.C. (1997). *Ecology and Management of North American Moose*. Smithsonian Institute Press, Washington, DC.

Hobbs, N.T. (1996). Modification of ecosystems by ungulates. *Journal of Wildlife Management*, **60**, 695–713.

Hobbs, N.T. (2006). Large herbivores as sources of disturbance in ecosystems. *Large Herbivore Ecology, Ecosystem Dynamics and Conservation* (eds K. Danell, R. Bergström, P. Duncan, & J. Pastor) Cambridge University Press, Cambridge, UK.

Holt, R.D. (2004). Implications of system openness for local community structure and ecosystem function. *Large Herbivore Ecology, Ecosystem Dynamics and Conservation* (eds. K. Danell, R. Bergström, P. Duncan & J. Pastor) Cambridge University Press, Cambridge, UK.

Huxel, G.R. & McCann, K. (1998). Food web stability: the influence of trophic flows across habitats. *American Naturalist*, **152**, 460–469.

Knight, T.M., McCoy, M.W., Chase, J.M., McCoy, K.A. & Holt, R.D. (2005). Trophic cascades across ecosystems. *Nature*, **437**, 880–883.

Larsen, J.A. (1980). *The Boreal Ecosystem*. Academic Press, London.

Likens, G.E. & Bormann, F.H. (1974). Linkages between terrestrial and aquatic ecosystems. *Bioscience*, **24**, 447–456.

Loreau, M. & Holt, R.D. (2004). Spatial flows and the regulation of ecosystems. *American Naturalist*, **163**, 606–615.

MacCracken, J.G., Vanballenberghe, V. & Peek, J.M. (1993). Use of aquatic plants by moose–sodium hunger or foraging efficiency. *Canadian Journal of Zoology*, **71**, 2345–2351.

McCann, K.S., Rasmussen, J.B. & Umbanhowar, J. (2005). The dynamics of spatially coupled food webs. *Ecology Letters*, **8**, 513–523.

McNaughton, S.J. (1985). Ecology of a grazing ecosystem: the Serengeti. *Ecological Monographs*, **55**, 259–294.

Moore, J.C., Berlow, E.L., Coleman, D.C., de Ruiter, P.C., Dong, Q., Hastings, A., Johnson, N.C., McCann, K.S., Melville, K., Morin, P.J., Nadelhoffer, K., Rosemond, A.D., Post, D.M., Sabo, J.L., Scow, K.M., Vanni, M.J. & Wall, D.H. (2004). Detritus, trophic dynamics and biodiversity. *Ecology Letters*, **7**, 584–600.

Naiman, R.J., Bilby, R.E., Schindler, D.E. & Helfield, J.M. (2002). Pacific salmon, nutrients, and the dynamics of freshwater and riparian ecosystems. *Ecosystems*, **5**, 399–417.

Odum, E.P., Finn, J.T. & Franz, E.H. (1979). Perturbation theory and subsidy-stress gradient. *Bioscience*, **29**, 349–352.

Olofsson, J., Stark, S. & Oksanen, L. (2004). Reindeer influence on ecosystem processes in the tundra. *Oikos*, **105**, 386–396.

Pastor, J., Dewey, B., Naiman, R.J., McInnes, P.F. & Cohen, Y. (1993). Moose browsing and soil fertility in the boreal forests of Isle Royale National Park. *Ecology*, **74**, 467–480.

Pastor, J., Cohen, Y. & Hobbs, N.T. (2006). The roles of large herbivores in ecosystem nutrient cycles. *Large Herbivore Ecology, Ecosystem Dynamics and Conservation* (eds K. Danell, R. Bergström, P. Duncan & J. Pastor), pp. 289–318. Cambridge University Press, Cambridge, UK.

Peterson, R.O. (1977). *Wolf Ecology and Prey Relationships on Isle Royale*. US National Park Service Scientific Monograph Series No. 11, US Department of the Interior, National Park Service, Washington, DC.

Peterson, R.O. (1995) *The Wolves of Isle Royale – A Broken Balance*. Willow Creek Press, Minocqua, Wisconsin.

Polis, G.A., Anderson, W.B. & Holt, R.D. (1997). Toward an integration of landscape and food web ecology: The dynamics of spatially subsidized food webs. *Annual Review of Ecology and Systematics*, **28**, 289–316.

Polis, G.A., Power, M.E. & Huxel, G.R. (2004). *Food Webs at the Landscape Level*. The University of Chicago Press, Chicago, Illinois.

Qvarnemark, L.M. & Sheldon, S.P. (2004). Moose grazing decreases aquatic plant diversity. *Journal of Freshwater Ecology*, **19**, 407–410.

Risenhoover, K.L. & Peterson, R.O. (1986). Mineral licks as a sodium source for Isle Royale moose. *Oecologia*, **71**, 121–126.

Ritchie, M.E., Tilman, D. & Knops, J.M.H. (1998). Herbivore effects on plant and nitrogen dynamics in oak savanna. *Ecology*, **79**, 165–177.

Sabo, J.L. & Power, M.E. (2002a). River-watershed exchange: effects of riverine subsidies on riparian lizards and their terrestrial prey. *Ecology*, **83**, 1860–1869.

Saugier, B., Roy, J. & Mooney, H.A. (2001). *Terrestrial global productivity*. Academic Press, London.

Stephens, P.W. & Peterson, R.O. (1984). Wolf-avoidance strategies of moose. *Holarctic Ecology*, **7**, 239–244.

Stottlemyer, R., Travis, B. & Toczydlowski, D. (1995). Nitrogen mineralization in boreal forest stands of Isle Royale, northern Michigan. *Water, Air, Soil Pollution*, **82**, 191–202.

Tischler, K.D. (2004). *Aquatic Plant Nutritional Quality and Contribution to Moose Diet at Isle Royale National ParK*. M. S. thesis. Michigan Technological University, Houghton, Michigan.

Vanni, M.J. (2002). Nutrient cycling by animals in freshwater ecosystems. *Annual Review of Ecology and Systematics*, **33**, 341–370.

Vucetich, J.A. & Peterson, R.O. (2004). The influence of top-down, bottom-up, and abiotic factors on the moose (*Alces alces*) population of Isle Royale. *Proceedings of the Royal Society B: Biological Sciences*, **271**, 183–189.

Wetzel, R.G. (2001). *Limnology (Lake and River Ecosystems)*. Academic Press, London.

Wilmers, C.C., Stahler, D.R., Crabtree, R.L., Smith, D.W. & Getz, W.M. (2003). Resource dispersion and consumer dominance: scavenging at wolf- and hunter-killed carcasses in Greater Yellowstone, USA. *Ecology Letters*, **6**, 996–1003.

Zackrisson, O., DeLuca, T.H., Nilsson, M.C., Sellstedt, A., Berglund, M. (2004). Nitrogen fixation increases with successional age in boreal forests. *Ecology*, **85**, 3327–3334.

Supporting information

Additional supporting information may be found in the online version of this article:

Appendix S1 Hobbs' (1996, 2006) urine and faecal nitrogen excretion models developed for large ungulates

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