We commonly think of ecosystem hierarchies in terms of productivity or trophic levels. Plants are considered primary producers, converting inorganic compounds to organic forms that can be consumed by secondary producers and others at higher trophic levels. However, we overlook the biophysical alterations by animals, particularly ecosystem engineers that influence habitat patchiness and the distribution of vegetative species (Burchsted et al 1997, Naiman and Rogers 1997). These alterations can also strongly influence system ecohydrology. Rather than a soil-plant-atmosphere continuum, ecohydrologists might consider a soil-animal-plant-atmosphere spectrum.

Rethinking Connectivity

Westbrook et al (2013) expand on the dialog initiated by King and Caylor (2011) by suggesting that ecohydrologists are not making use of the strengths of their parent disciplines by focusing on plant-water interactions – the least demanding common subject for ecology and hydrology. Using two independent data sets of articles, the authors conducted a bibliographic survey of ecohydrological articles in two databases, identified general themes and assigned topical classifications. Macroinvertebrate and vertebrate fauna were subdivided into two classes as either those impacted by hydrologic processes or those impacting hydrologic processes. Biogeochemistry was assigned a class, including climate impacts on soil. Humans were classified separately from animals to distinguish anthropogenic from non-anthropogenic interactions. One final class was assigned to plant-hydrology interactions. The authors found that the majority (72%) of ecohydrology articles addressed vegetation and hydrology interactions. The majority of faunal articles were about the impact of hydrologic processes on fauna. Less than 7% of ecohydrological articles focused on faunal impact on hydrologic processes and included topics such as bioturbation and soil-water balances, and the influence of beetles on transpiration. Westbrook et al. (2013) believe the emphasis of ecohydrology is on plants because the founders of ecohydrology were either plant ecologists or hydrologists who research processes mediated by plants. A more accurately named blended discipline of “botanohydrology” is proposed (Westbrook et al. 2013).
Ecology implies living systems which include plants and animals so why is the emphasis of ecohydrology on plants? Animal ecologists are less familiar with the principles and methods of hydrology and there have been few studies on animals as drivers of hydrological processes. As manipulators of biogeochemical systems, ecosystem engineers influence and regulate hydrologic processes and fill the gap at the intersection of hydrology and animal ecology (Westbrook et al. 2013).

Vertebrate and invertebrate ecosystem engineers such as alligators, beavers, earthworms, and crayfish can have direct hydrologic process impacts through activities such as damming, trampling and burrowing. As a result changes occur in water quality, water table levels, suspended sediment loads, soil moisture levels, etc. Indirect animal impacts through activities such as herbivory, pollination, seed dispersal, and nutrient input can result in a cascade of changes in vegetation cover, energy balance, evaporation, soil moisture levels, etc. (Westbrook et al. 2013). Animal activities influence almost every aspect of the hydrologic cycle and abiotic factors of soil-moisture balance such as soil porosity, interception and evapotranspiration, overland flow and runoff, infiltration and soil moisture storage, and groundwater recharge and flow. A quantification of the scale of faunal hydrologic influence can be incorporated into numeric models to simulate ecohydrological conditions (Westbrook et al. 2013).

Expanding on the recommendations of Hannah et al. (2004) a truly interdisciplinary integration of ecohydrology’s parent disciplines will need to additionally incorporate all of the “eco” of ecology and also not default to “lazy” research strategies (King and Caylor 2011). As a first step, forming an interest group on fauna in ecohydrology can stimulate discussion and allow the discipline to grow (Westbrook et al. 2013). Unfortunately, to date, the article by Westbrook et al (2013) is only cited by two published articles. It would seem that the desired dialogue has not yet begun.

**Impact of Faunal Ecosystem Engineers**

Natural rivers flow in meanders, riffles and pools, and fits and starts, and migrate and evolve over time. Beaver activities alter biogeochemical cycles, hydrologic processes and sediment transport regimes, emulating heterogeneous natural processes and discontinuities by creating a mosaic of riparian habitat patches consisting of free-flowing river segments, in-channel and valley impoundments, ponds and meadows. (Burchsted et al. 2010).

The actions of organisms known as “ecosystem engineers” influence patch heterogeneity. While many organisms were considered in coining the term “ecosystem engineer,” beavers are a strong example of allogenic engineers, altering both biotic and abiotic materials in the environment (Jones et al 1994). An assessment of longitudinal discontinuities in streams found that intact beaver dams are the most naturally discontinuous fluvial structure (Burchsted et al. 2010).
Burchsted et al. (2010) used a hierarchical patch dynamics (HPD) model to compare the discontinuity of free-flowing, beaver impoundments, and beaver meadows segments at hierarchical scales (reach, segment and river network) of three-dimensional patches in longitudinal, lateral and vertical views. Various stream parameters were used to compare the structure and function of each. Major differences were found in segment-scale sediment transport, organic material storage and accumulation rate, channel shape and channel bed material size. Segments also varied temporally with beaver dams persisting for decades to centuries and beaver meadows persisting from centuries to millennia. The authors stress the need to understand processes at the catchment scale (Burchsted et al. 2010).

The conceptual model presented by Burchsted et al. (2010) can be used to inform stream restoration efforts and frame related research questions. The authors offer a long list of suggested testable hypotheses that address natural flow regime, channel geomorphology, biota and water quality. Differences in process and channel morphology affect the catchment sediment budget. Anticipated sediment variations include transport or erosion in free-flowing segments, erosion in beaver meadows, and deposition in beaver impoundments. Overall species biodiversity and the presence of rare species is expected to increase in beaver-modified systems. Nutrient cycling is both enhanced and limited by beaver engineering activities. In general, heterogeneity in beaver-colonized systems is expected to impart resilience in response to nutrient input fluctuations (Burchsted et al. 2010).

Of greatest interest to ecohydrologists are predictions of beaver impact on the natural flow regime. Water impounded by beaver dams enhances surface storage and groundwater recharge. Anticipated hydrologic responses are increased high flow duration, increased baseflows, and reductions in drought duration and frequency. However, baseflow rates fall in some beaver-colonized systems, possibly due to forest transpiration, evaporation from impoundments, and aquifer groundwater storage and release capacity (Burchsted et al. 2010). Previous readings suggest precipitation rates and regional geology may influence baseflow rates (Jackson et al. 2005, Wilcox and Huang 2010). Stormflow rates will vary with soil saturation levels. In general, beaver dams increase the stochasticity of storm response and influences on the natural flow regime (Burchsted et al. 2010).

Discontinuity is innate to fluvial and riparian systems and should be taken into consideration in restoration activities. Network-scale improvements should include variability of sediment.
storage and release, water levels, patch heterogeneity and discontinuity-generated processes (Burchsted et al. 2010). The authors argue against the standard practice using of existing reference conditions as a restoration template and also the scale at which assessments are made – rather than reach-scale restoration, impacts on and influences of the entire catchment should be considered. Reference conditions are natural analogs that are used as templates to inform restoration strategies. The river continuum concept (RCC) to which they refer is a model, not a reference condition, and is outdated. Dave Rosgen, who developed the reference reach and natural channel design concepts had great influence in the 1990s but his methods have more recently met with criticism (Lave 2015).

Naiman and Rogers (1997) are also concerned with the status quo of management strategies that emphasize constrained linear river channels devoid of variability and lacking animals. Influenced by primary processes, riparian corridors have spatial and temporal variability which results in heterogeneity of plant and animal habitats. Naiman and Rogers (1997) place the biophysical alterations of large animals as a hierarchical second level of influence on river corridor structure and dynamics, following primary chemical and physical processes and preceding nutrient cycling and elemental distribution (commonly considered plant processes). Large animals such as beaver, moose, crocodile, elephant, and hippopotamus further modify habitat patch dynamics and spatio-temporal variability with activities such as burrowing, damming, wallowing and herbivory, altering microtopography, vegetative structure, and channel morphology, and functions such as resistance and resilience to disturbance, connectivity and productivity (Naiman and Rogers 1997).

Naiman and Rogers (1997) place animals into functional groupings according to patch-level effects from their activities. The geomorphology of rivers and riparian vegetation are influenced by ponding, digging, and trampling. Ponding alters local hydrology and patch heterogeneity is influenced by feeding activities that modify the vegetative community. Feeding strategies of herbivores can alter plant community structure, soil development, and species associations. Animals that may seem very different can have functional similarities. North American beavers and southern Africa hippopotamus both modify hydraulic conditions. Beaver dams retain water and large amounts of sediment whereas hippopotamus wallowing and movements create canals, deepen pools and stir up sediment. Additional activities of both animals result in habitat patches that are spatially and temporally variable (Naiman and Rogers 1997).

Strategies that optimize conditions for individual species fail to consider the similarities and differences in functional groupings when making management decisions. Identifying animal ecosystem functions can facilitate the integration of wildlife management with river management. Nutrient cycling and retention, spatial and temporal heterogeneity,
connectivity, biodiversity, productivity and disturbance regime are all influenced or modified by animals as key “engineers” of riverine ecosystems (Naiman and Rogers 1997).

The science of ecohydrology can certainly be more “eco” by including animals in an interdisciplinary continuum of atmosphere-plant-animal-soil systems across scales, particularly in light of global change. Climate change is expected to move faster than plants can migrate. Because animal response to stimuli is much more rapid than plants, they can adapt to change quickly (Westbrook et al. 2013). But why stop there? Why not include humans in the continuum? What about fungi or microorganisms? Surface water, groundwater and rainwater are all hydrologically connected. Just so, there is ecological connectivity between all living organisms and their environment.

References:


