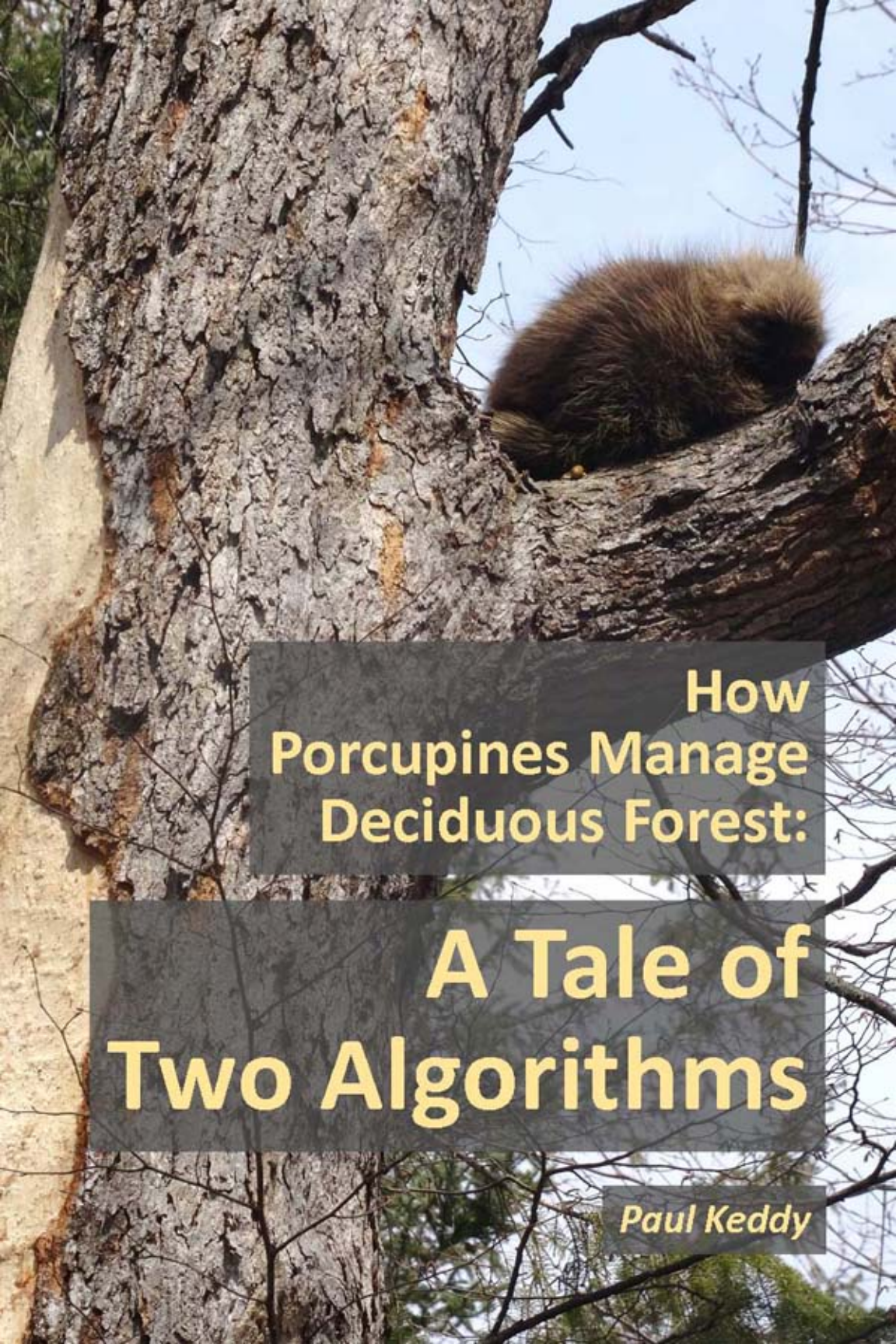
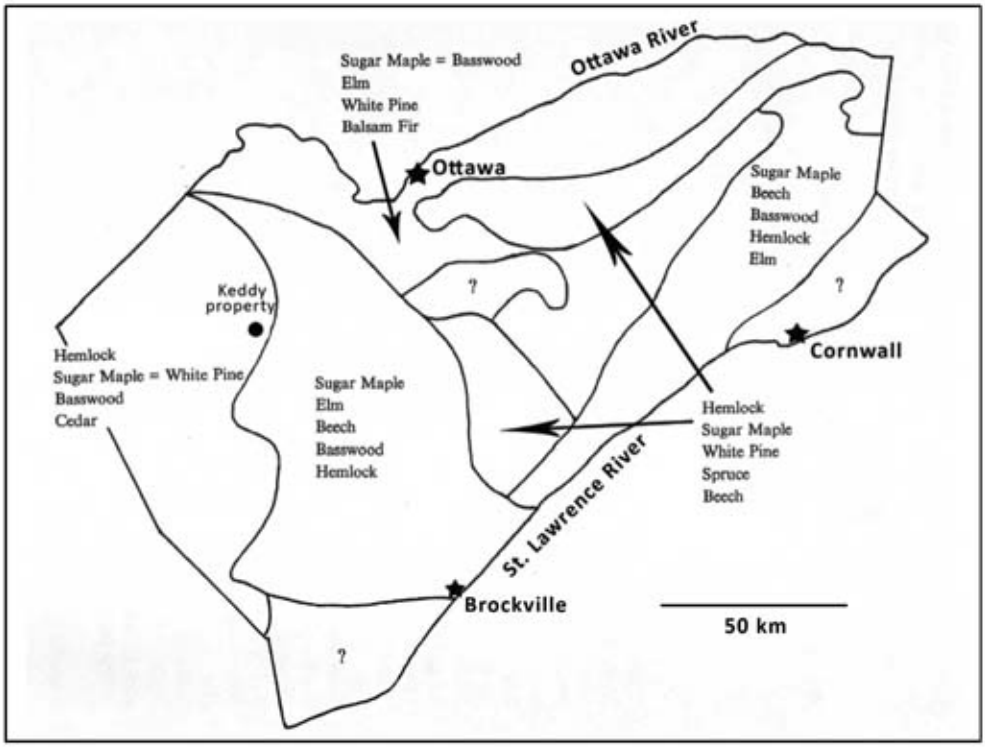


How Porcupines Manage Deciduous Forest:

A Tale of Two Algorithms

Paul Keddy

The Ottawa Valley was once covered by dense forest. The dominant trees were maple, oak, pine and hemlock. We know this from sources including pollen records from lake sediments and records made by early surveyors. Using such information, we can even map the original forests of this region (see Map 1). Our forests here have now suffered from several hundred years of human abuse, including logging, clearing for farms, multiple cycles of firewood cutting, and grazing by cattle. So, when we have a piece of forest to manage now, we have roughly three choices: (1) we can continue the cycle of abuse, taking whatever we can whenever we can, (2) we can stop any active management and let the forest recover in a more or less random way, or (3) we can quite deliberately try to actively manage it in a way that helps restore it to a composition that was typical of the pre-settlement era. I have been trying to do the latter with my own piece of forest, which comprises some 500 acres west of Ottawa. Of course, there are other species that also have their own views on forest management, including beavers, porcupines and while-trailed deer.



Map 1. *The tree species (in order of relative abundance) in upland forests of each physiographic region of Eastern Ontario prior to European settlement. These were mapped by Cathy Keddy based upon surveyors' notebooks stored at the Survey and Mapping Branch of the Ontario Ministry of Natural Resources (Keddy, C.* Forest History of Eastern Ontario. *Information Report No. 1. Eastern Ontario Model Forest, Kemptville, Ontario, 1994.) Table 1 in this report shows that the three dominant trees in till and rock landscapes were maple, hemlock and white pine. Other common species included beech, elm, basswood, ash and white cedar.*

Previous page: *A porcupine lounging on a branch of its feeding tree, Keddy Nature Sanctuary, April 9, 2017.*

First a note on my own forest management for the 600 acres we own. For some forty years, I have applied a well-honed algorithm for forest restoration and firewood cutting. My first objective is to restore a closed forest canopy, to ensure that the ground is shaded again. Shade is necessary for native spring wild flowers to replace the mostly exotic grasses and forbs found in old fields. A forest canopy also allows interior forest birds to breed, and it ensures that mostly shade-tolerant trees regenerate from seed in the future. My second objective is to try and recreate a more natural canopy composition, which should then benefit all the other wild species that live in this forest. The long term goal is to allow the forest to recover to the natural composition it likely had back before logging and settlement changed it. Since it took some two centuries for the process of degradation to occur, I am aware that my current work must patiently nudge the forest back in the right direction, accepting that the final desired result will not occur in my lifetime. I hope one day the forest will look like ancient forest, perhaps like one of the fine older stands in Algonquin Park or Gatineau Park.

The current forest is very different from the original pre-settlement forest, which was dominated by sugar maple, American beech, red oak, eastern hemlock and white pine. We know the composition of these original forests from Cathy Keddy's work using notebooks kept by land surveyors (Map 1). The current forests are now dominated by ironwood, white spruce, white birch and poplar, and there are scattered clearings that have few trees at all. How does one begin to restore a degraded forest and to generate firewood? The first rule in my algorithm is to find two healthy young trees closer than eight feet from one another. In order to increase rates of growth, one of the two must go, and one can stay. Which tree to keep? First to keep are those tree species mentioned above that were important canopy trees in natural deciduous forests: sugar maple, American beech, red oak, eastern hemlock and white pine. (I am not sure why red oak is not more prominent in Cathy Keddy's report but I think there are good ecological reasons to assume it was an important species in some locations, at least on the rock ridges that typify our protected forest.) Another list of keepers are trees that are relatively rare on our property: butternut, bur oak, black cherry, yellow birch and bitternut hickory. By far the commonest tree on our property is ironwood, a midsize tree that is relatively tolerant of drought and poor soils. I suspect the abundance of ironwood reflects past forest uses, such as selective removal of maple and oak for firewood and grazing by cattle. Ironwood seedlings are usually left by herbivores (much more on this topic below). So, when I am marking trees for firewood, usually my cutting decisions are straightforward: one tree an ironwood, the other a sugar maple? Cut the ironwood. Occasionally the algorithm fails: what to do if one tree is an American beech, and the other a black cherry? In such a case, the algorithm recommends keeping both. This also provides a margin of safety, since it is reasonable to assume that in a coming decade, an ice storm or another falling tree or a beaver will make the choice for me.

Left: *Beavers selectively remove trees such as red oak, sugar maple and beech. Here's one on our House Pond on April 7, 2015.*

Still lounging... and watching!

I have applied this simple algorithm over hundreds of acres for four decades, getting healthy exercise and heating my house. I am pleased to report that the forest looks much more like the original forests of Lanark County than when I began stewardship. More importantly, as the surviving trees grow in the coming decades, and produce new generations of seedlings, we will have something better than the typical degraded, second growth forests you often see in farm woodlots around Lanark County. We are such optimists that we have provided our local land trust with a mixture of a conservation easement and outright land gift so that no one will be able to log or subdivide or otherwise harm these forests in perpetuity, beginning with the next 999 years. So, taking the expansive view, our tree removal for wood heating is going to leave a vastly more natural forest for future generations of wild creatures.

Our woodpile tangibly illustrates the progress. It shows the output from my algorithm. That is, it is a highly selective woodpile. We heat with the species that are least desirable in a restored forest.

What could go wrong with this plan? It has become apparent that a group of my neighbours has a different algorithm to guide their use of the forest. These neighbours are porcupines, and there is a rather large population of them. I can think of at least ten trees which are porcupine dens. A single enormous butternut, for example, houses at least three. Porcupines, like most herbivores, are quite selective about their food. They don't generally eat wood, because wood is mostly cellulose. Rather, they eat tree bark, because the cambium in the bark has higher levels of nitrogen and phosphorus. These are two critical nutrients for animal growth, and nearly all herbivores have a preference for tissues with high nitrogen levels – cambium, buds, and seeds. This selectivity in herbivores is a world-wide phenomenon, and I have written a full chapter on it in my latest book, *Plant Ecology*.

Porcupines, like goats, elephants, or tortoises, can be very selective in their diet. Hence, porcupines have their own algorithm for forest management, and it is quite different from mine. Give them a pair of trees, and the decision goes something like this: if it is ironwood, leave it alone. If it is maple, oak, or beech, remove the bark. If it is hemlock, remove the foliage in the winter. As you can immediately see, their algorithm is not only different, but almost exactly the opposite of mine. They keep the ironwood, and remove the maple, oak, and beech.

This process was driven home during the winter of 2017-2018 on a rock ridge not far from my house. Here was a piece of forest which I had been managing by my own algorithm for several decades. In this stand of forest, an ancient basswood tree, part of which is hollow, provides shelter for at least one, and possibly more, porcupines. This winter, radiating out into the forest from this ancient tree, there was a network of trails in the snow. At the end of each trail was a debarked maple tree. Nearly every week would reveal a new trail and a new heavily-grazed maple tree. In just one winter, more than a dozen maple trees, each about thirty years old and growing vigorously, had been debarked extensively, likely enough to kill the tree. In just one winter, then, the forest composition has been strongly pushed back to being an ironwood-dominated rock ridge. As if to finish the task, there were also several young hemlock trees that I had carefully observed and tended. They were half stripped of foliage too, including the top branches where growth would be most important.

I understand, of course, that porcupines eat bark, and have seen many examples of this over my lifetime. But this winter drove home how selective porcupines are in their feeding, and how rapidly they can change the composition of a forest. It is obvious now, as you can see the whitish trunks of the debarked maple trees, somewhat like skeletons standing in the forest. If you fast forward twenty years, the porcupines may be long gone. Perhaps they will have exhausted their food, or have been eaten by fishers. But their effects will still be in evidence – the maples will be gone, and ironwood forest will continue to dominate this rock ridge. Will future biologists wonder what created such a forest, and perhaps treat it as a consequence of shallow soil, or drought, or even climate change? Moreover, it is not just one rock ridge – it seems likely that the same process is occurring around each porcupine den in our forest.

Left: *A young sugar maple debarked by porcupines.*

It is not just porcupines. The forests here have another herbivore working through them in a similar way, with trails radiating outward not from a hollow tree, but from a nearby pond. For a decade, our ponds have had resident beaver families. The beavers seem to have food preferences similar to porcupines, as evidenced by the stumps of sugar maple, red oak and beech. When beavers get really hungry, they will turn to ironwood, although it is my impression that ironwood is mostly used for construction purposes. It would seem its bark is mostly a food of desperate last resort. Since the 1970s, when beaver populations seem to have been highest, they have eaten through the surrounding forest, removing their preferred food trees, leaving ironwood and white spruce. Eventually they disappeared from many of the ponds, probably because the food supply was insufficient. Once again, while my algorithm removes ironwood and white spruce, their feeding algorithm leaves both these species.

Then we have white-tailed deer. The current population density of deer is vastly above what the forest can really support. Eight "white-tailed" over-wintered on just one ridge near our home. During this winter they removed nearly all the terminal buds on any sapling or seedlings less than four feet tall. The skeletons of these small trees are still there, but they simply have no buds. Each tree struggles to produce new buds and branches in the summer, but the deer remove these new shoots as well. The forest understory, therefore, consists mostly of deformed young trees awaiting death. It will interest you to know that there is one species that deer seem to avoid – ironwood.

Deer eat nearly all species of young trees, and most native shrubs, but they generally leave ironwood.

It is becoming increasingly apparent to me, then, that my landscape is dominated by ironwood for a good reason. We are now living in an herbivore-dominated landscape. I was trained to think that our forests are mostly controlled by soil depth and soil moisture; perhaps the herbivores matter more. In the past, in pre-settlement forests (Map 1), porcupines were likely consumed by fishers and bobcats. A few fishers have, indeed, returned to our region (we see their tracks in the winter), but apparently there are not enough of them to reduce the porcupine population. In the past, deer and beaver may have been controlled by wolves and cougars. Now we have neither of these large predators. We do have coyotes, and each winter we see the remains of several carcasses left by them. Of course, this does not mean that the coyotes even killed those deer. Perhaps they mostly consume deer that died of natural causes. In any case, the abundance of deer tracks and the

damage from deer feeding shows that coyotes are simply not up to the task of controlling herbivores. Looking ahead, I find it hard to imagine that fishers, bobcats, wolves and cougars will soon resume their vital work of protecting forests from herbivores.

Even our oldest and most natural tracts of forest on this property may now be changing under steady pressure from herbivores. These areas of forest have a canopy of maple, oak, beech and hemlock. Trees occasionally die, of course. Each such gap is where the future of the forest lies. If you look carefully at what new young trees are establishing in gaps, you can forecast the trees that will occur decades or even centuries into the future. When a gap occurs and tree seedlings establish, the deer remove nearly all the seedlings except ironwood. We therefore have small clusters of ironwood emerging under our oldest maple, oak and beech trees. Occasionally a few young maples or hickory hide within those ironwoods; they offer some hope. Of course, these trees are still less than ten feet tall. Soon they will be large enough for the porcupines to find!

A young oak tree partially debarked by porcupines.

In short, we have three dominant herbivores, all abundant, and all with a forest algorithm quite different from mine. I thought for a few decades that my algorithm, focussed upon restoring our landscape to its original composition, might direct the next centuries of tree composition, and leave a lasting positive impact on this landscape. It would seem, rather, that the porcupines will win, aided as necessary by the deer and beaver. They have their own plan for the future: ironwood-dominated rock ridges, with white spruce in the valleys. We will have to ask our grandchildren to report on whose plan has been carried to fruition. Meanwhile, I have learned a valuable lesson from our winter porcupine: never underestimate the power of herbivores to shape forests and landscapes.

All photos were taken by Cathy Keddy.

About the author: Paul Keddy (www.drpaulkeddy.com) is a biologist and author living in Lanark County. His latest book is Plant Ecology: Origins, Processes, Consequences, *Second Edition, 2017, with Cambridge University Press. He and his wife, Cathy Keddy, are stewards for Keddy Nature Sanctuary, one of the larger properties protected by the Mississippi Madawaska Land Trust.*

Left: *A porcupine taking refuge in a hollow tree during the winter.*