

Sugar maple and nitrogen cycling in the forests of eastern North America

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Sugar maple (*Acer saccharum*) is the most dominant and widely distributed tree species of the northern hardwood forests of the northeastern US and southeastern Canada. Recent studies have shown that sugar maple is also a unique and critical species with regard to nitrogen cycling in forest ecosystems, because forest stands dominated by sugar maple tend to have high rates of nitrification and nitrate leaching to surface waters. In some areas, sugar maple populations may be increasing due to reduction of one of their main competitors, American beech (*Fagus grandifolia*). However, several factors threaten populations of sugar maple in the near future, including acid deposition, climate change, and the introduction of a new insect pest. Changes in the abundance of sugar maple could lead to major alterations in nitrogen retention by forested watersheds in eastern North America.

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In eastern North America, the glow of a sugar maple-covered hillside in full autumn color is an unforgettable sight. Sugar maple (*Acer saccharum*) (Figure 1) is one of several major tree species of the northern hardwood forest, along with American beech (*Fagus grandifolia*), yellow birch (*Betula alleghaniensis*), eastern hemlock (*Tsuga canadensis*), and several other hardwood and conifer species (Bormann *et al.* 1970). Found as far south as Alabama and as far west as Wisconsin (Little 1971), in the center of its range (southern Ontario and Quebec, New England and New York) sugar maple is often the dominant tree species in the forest (Alerich and Drake 1995; Griffith and Alerich 1996; Frieswyk and Widman 2000a, 2000b). In addition, sugar maple is one of the most valuable timber species of the northern hardwood forest and supports a maple syrup industry that sells about \$100 million worth of syrup annually from the northeastern states and Canada (Allen *et al.* 1995). Tapping sugar maples for sap to produce syrup has a long history dating back to the Native Americans (Wittstock 1993), and maple syrup became an important source of sweetener for European

settlers in the region (Figure 2).

However, the importance of sugar maple extends well beyond its association with fall colors and pancakes. Recent studies show that, among the trees of the northern hardwood forests, sugar maple has unique characteristics that exert a strong influence on nitrogen (N) cycling and retention (defined as atmospheric input of N minus gaseous and hydrologic outputs) in forested watersheds. The effect on N retention is very important because this region receives high levels of atmospheric N pollution from fossil fuel combustion in urban and industrial areas of the US East Coast and Midwest. If this atmospherically deposited N is not retained by forest ecosystems, but instead is leached through the forests to the surface waters, it can acidify soils, streams, and lakes, and pollute estuaries and coastal waters (Aber *et al.* 2003).

■ Sugar maple and nitrogen cycling

Recent research has shown that, compared to the other dominant species in the northern hardwood forest, sugar maple is more often associated with soils with high rates of nitrification and nitrate production. Nitrate is the most mobile form of inorganic N in soils and is more readily lost from ecosystems by leaching into ground and surface waters. For example, in a comparison of single-species plots of five major tree species in the Catskill Mountains of southeastern New York state, soils under sugar maple had the highest rates of net nitrification in laboratory incubations and the highest levels of extractable soil nitrate compared to soils associated with the other tree species (Figure 3, Lovett *et al.* in press). Similar high rates of net nitrification were found under individual trees of sugar maple in western Connecticut (Finzi *et al.* 1998a), and in sugar maple-dominated stands in eastern Wisconsin (Pastor *et al.* 1984), Michigan (Zak

In a nutshell:

- Sugar maple plays a critical role in regulating nitrogen leaching from forested watersheds in eastern North America
- Soils under sugar maple stands tend to promote the formation of the highly mobile nitrate ion
- Changes in sugar maple populations are likely in some areas in the next few decades due to anthropogenic stresses
- Increases in sugar maple abundance should lead to lower N retention in forested watersheds, while decreases in sugar maple should result in higher N retention

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Courtesy of Gary Lovett

Figure 1. Sugar maple in autumn color in the Adirondack Mountains, NY.

et al. 1989), and across the northeast (Lovett and Rueth 1999, Ross *et al.* in press). Sugar maple stands may also have high rates of gross nitrification (the rate of production of nitrate by nitrifying bacteria), (Verchot *et al.* 2001), but it is the net nitrification rate (gross nitrification minus consumption of nitrate by microorganisms and abiotic processes in the soil) that ultimately dictates the availability of nitrate for plant uptake and nitrate loss via leaching. Higher nitrate leaching results in lower N retention by the ecosystem.

The characteristics of sugar maple that produce high net nitrification rates in soil are not completely understood. Compared to other deciduous species, sugar maple does not have unusually high nitrogen concentrations in its foliage or wood (Lovett *et al.* in press; Templer *et al.* in press). However, its foliar litter does have low lignin concentrations and a low lignin:N ratio, leading to high rates of decomposition (Melillo *et al.* 1982; Pastor and Post 1986; Lovett *et al.* in press). Consequently, the soil organic matter that develops under sugar maple stands tends to have a low carbon:nitrogen (C:N) ratio (often in the range

14–18) (Lovett *et al.* in press) which can lead to high rates of net nitrification (Lovett and Rueth 1999; Goodale and Aber 2001; Aber *et al.* 2003). In mixed-species plots in the Catskill Mountains of New York, the White Mountains of New Hampshire, and the Appalachian Mountains of West Virginia, abundance of sugar maple was significantly correlated with lower soil C:N ratios or higher rates of net nitrification or both (Christ *et al.* 2002; Lovett *et al.* 2002; Ollinger *et al.* 2002; Venterea *et al.* 2003).

Other unusual aspects of sugar maple physiology may also be involved in its effect on soil N cycling. First, while sugar maple occurs on soils with a wide range of pH and base cation levels, it often does poorly in soils that are low in calcium and magnesium, high in aluminum, and have low pH (Burns and Honkala 1990, Van Breemen *et al.* 1997). The addition of lime increases the survival, vigor, diameter growth, and seed production of sugar maples in base-poor sites (Long *et al.* 1997). Sugar maple may be able to maintain high calcium in its tissues and in surface soils by using deep roots to access calcium from lower soil horizons (Dijkstra and Smits 2002). It is possible that the high nitrification rates under sugar maple stands are a response to the higher pH of the soil rather than any aspect of the litter quality (Paul and Clark 1996). However, Lovett *et al.* (in press) found that among the five major species in the Catskill Mountains, the highest pH values (in mineral horizons) were found under sugar maple and red oak stands, the species with the highest

and lowest net nitrification rates, respectively. This suggests that although the abundance of sugar maple may be



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Figure 2. Maple syrup production in New England in the 19th century. Buckets were used to haul the maple sap to a saphouse where it was boiled down to produce maple syrup.

enhanced in soils of high base status, the higher soil calcium and pH values do not necessarily produce the high nitrification rates. Second, sugar maple trees are “hydraulic lifters” that transport water from deep soil and release it into surface soils at night, following a gradient of water potential (Dawson 1993). This process tends to keep surface soils moist during dry periods, which may enhance soil microbial N cycling, including nitrification. Third, sugar maple has arbuscular mycorrhizae, in contrast to beech, oak, hemlock, and birch, which have ectomycorrhizae (Blum *et al.* 2002). Ecto- and arbuscular mycorrhizae differ in N cycling properties (Langley and Hungate 2003). However, the relationships between these physiological characteristics and the unusual properties of soils that develop under sugar maple have not been thoroughly explored.

Because sugar maple does not readily take up nitrate (Rothstein *et al.* 1996; Templer 2001; Templer and Dawson in press), high rates of net nitrification and nitrate production can lead to high rates of nitrate leaching from soils. Nitrate leaching contributes to the depletion of nutrient cations from forest soils, acidification of streams and lakes, and eutrophication of estuaries and coastal waters (Murdoch and Stoddard 1992; Driscoll *et al.* 2003; Aber *et al.* 2003). In the mixed-species forested watersheds of the Catskill Mountains, stands with a higher abundance of sugar maple have lower C:N ratios in organic horizons of the soil which are associated with elevated concentrations of nitrate in drainage waters (Lovett *et al.* 2002). In sites across the Adirondack Mountains of northern New York State, there is a positive relationship between the abundance of sugar maple in the study plots and the concentrations of nitrate in soil solution below the rooting zone (Figure 4). The presence of nitrate below the rooting zone is generally considered an indicator of N loss from forest ecosystems. In a comparison between forested sites in the Turkey Lakes watershed of eastern Ontario, Canada, and Huntington Forest of the Adirondack Mountains in New York State, Mitchell *et al.* (1992) found higher rates of nitrate leaching in Turkey Lakes despite lower rates of atmospheric N deposition; the authors attributed this pattern to a higher abundance of sugar maple and an absence of American beech. Furthermore, soil freezing events may stimulate more nitrate loss from soils under sugar maple than other tree species (Boutin and Robitaille 1995, Fitzhugh *et al.* 2001).

One could question whether the soil properties under sugar maple stands are a cause or an effect of the presence of sugar maple on the site. In other words, do sugar maple trees create the soil properties conducive to their growth or do they tend to grow on soils with these properties? The best way to distinguish the cause and effect of plant–soil relationships is through a common garden experiment, in

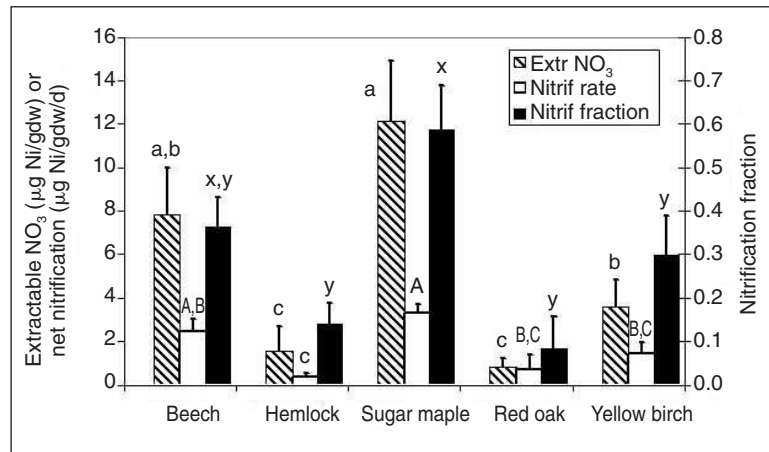


Figure 3. Mean concentrations of KCl-extractable nitrate in organic horizon soils (Oe and Oa horizons, striped bars), rates of net nitrification (white bars), and nitrification fraction (ratio of net nitrification to net N mineralization, black bars) for single-species plots of five dominant species in the Catskill Mountains of New York. Bar heights represent means of six plots per species; error bars are the standard error of the mean. Letters indicate statistical comparison of means of these response variables using analysis of variance. For each response variable, species sharing a letter are not significantly different ($P > 0.05$). Redrawn from data in Lovett *et al.* (in press).

which trees of different types are planted on the same soil and allowed to mature. While there are notable examples of such experiments in the literature (Son and Gower 1991; France *et al.* 1989), none have involved sugar maple. However, several aspects of the comparative studies cited above suggest that sugar maples cause, rather than respond to, low C:N ratios and high net nitrification rates. First, the soil C and N characteristics are often seen most strongly in the organic horizons rather than the mineral horizons, suggesting that it is the organic matter produced by the tree that causes the characteristic, rather than some property of the underlying substrate. Also, these C and N characteristics are observed under mature trees, and the soils under those trees have had decades to respond to the organic matter produced by the maples. If the trees did not create, or at least perpetuate, the C and N effects, the effects should disappear after decades of organic matter turnover. Finally, similar effects are observed in many locations across a broad range of bedrock and superficial geologies, again suggesting that underlying substrate is not the cause. The situation is different for calcium, however, because there is good evidence that sugar maple both responds to, and modifies, the calcium status of a site (Van Breemen *et al.* 1997; Finzi *et al.* 1998b; Bailey *et al.* in press).

Sugar maple may not be unique in its effects on soil N cycling. Mitchell *et al.* (2003) considered sugar maple to be part of a suite of species, including basswood (*Tilia americana*), eastern hophornbeam (*Ostrya virginiana*) and white ash (*Fraxinus americana*) that prefer base-rich soils and are associated with high nitrate production in soils. High net nitrification rates have been measured in soils

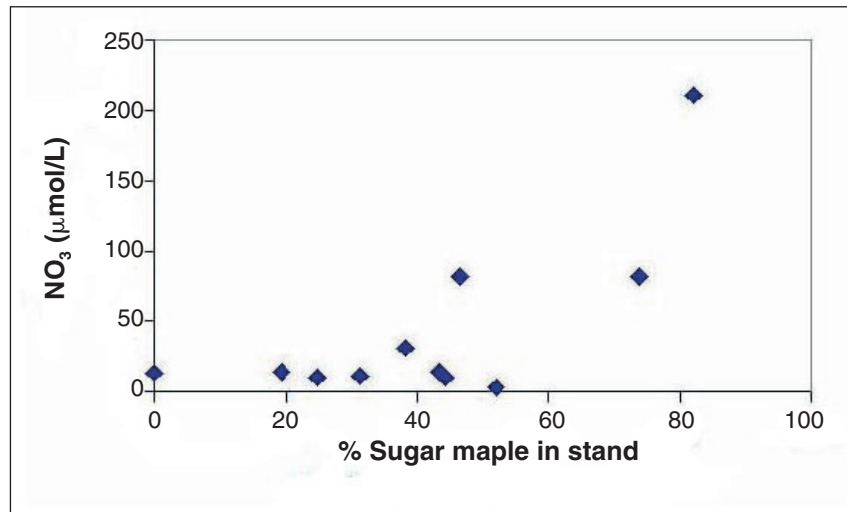


Figure 4. Concentration of nitrate in B-horizon soil solution in mixed-species stands in the Adirondack Mountains of New York State, plotted against the percentage of sugar maple in the stand (Mitchell *et al.* 2003). These soil solution samples are from a depth largely below the rooting depth of the trees, so the nitrate present in the water at this depth is considered an index of the amount of nitrate lost from the plot by leaching. These data indicate that increased nitrate leaching is observed in stands having more than about 50% sugar maple.

under white ash in Connecticut (Finzi *et al.* 1998a), and Zak *et al.* (1989) found sugar maple–basswood–white ash forests to have much higher net nitrification rates than the other stand types they surveyed in Michigan. Within this suite of species, however, sugar maple is by far the most dominant and therefore has the greatest influence on ecosystem nutrient cycling over large regions.

■ Changes in sugar maple abundance

In New York State and northern New England, sugar maple appears to be holding its own in competition with other tree species. Records from the USDA Forest Service Forest Inventory and Analysis (FIA) program show that sugar maple is the most dominant hardwood tree (in terms of tree volume) in Vermont and New York, and the second most dominant, behind red maple (*Acer rubrum*) in Maine and New Hampshire (Alerich and Drake 1995; Griffith and Alerich 1996; Frieswyk and Widman 2000a, 2000b). In each of these states, sugar maple volume as a fraction of total hardwood volume did not change appreciably between FIA measurements in the early 1980s and the mid-1990s. In a study of the mortality and crown conditions in 223 sugar maple-dominated stands in the northeastern and north-central US and eastern Canada from 1988–1997, Allen *et al.* (1999) reported that sugar maple mortality was typical of trees found in northern hardwoods stands. Areas of high sugar maple mortality have often been associated with recent drought or insect attack (Kolb and McCormick 1993; Allen *et al.* 1999).

Despite the apparent stability of sugar maple populations over the past several decades, the future of sugar

maple is uncertain because of a number of simultaneous and potentially interacting changes occurring in northern hardwood forests. One major factor that could affect sugar maple is the increased mortality of one of its principal competitors, American beech (*Fagus grandifolia*), due to beech bark disease. This disease complex is caused by a scale insect (*Cryptococcus fagisuga*) and fungi of the genus *Nectria*. It was introduced to North America at Halifax, Nova Scotia around 1890, and has since spread through the Maritime Provinces of Canada and the northeastern US, southwest to Ohio, and as far south as Virginia (Houston *et al.* 1979; Houston 1994). A decline in beech and a resulting increase in sugar maple may well be occurring in the Catskill Mountains of southeastern New York, where beech bark disease is ubiquitous (Griffin *et al.* 2003), and forests that were dominated by beech in pre-settlement times are now dominated

by sugar maple (McIntosh 1972). Manion and Griffin (2001) reported that beech in the Adirondack Mountains of northern New York suffered unusually high mortality because of beech bark disease, and that the beech decline resulted in an increased abundance of sugar maple and red maple. In some other areas, beech appears to be able to maintain its dominance despite the disease, although the age and size structure of the populations are affected. At Huntington Forest in the Adirondacks, Forrester *et al.* (2003) found that beech bark disease is having a dramatic influence on the demography of beech, with older, larger trees declining and young beech saplings increasing in density. Another prominent species of the northern hardwood association, eastern hemlock, is also currently under attack from an introduced insect, the hemlock woolly adelgid (*Adelges tsugae*) (Orwig and Foster 1998). Thus, one might expect that, in some areas of the northern hardwood forest, populations of sugar maple could increase in the near future due to the devastating effects of these introduced pests on its competitors. On the other hand, sugar maple is itself threatened by a number of anthropogenic stresses with potentially very serious consequences. We discuss three stresses below in what we believe to be the order of increasing threat.

First, there may be adverse effects of acid deposition on sugar maple, especially in sites with low soil base cation content. Acid deposition is associated with increased sulfate and nitrate leaching from soils, and flux of these anions engenders an equivalent loss of cations. Depending on the cation exchange properties of a soil, these fluxes of mobile anions can accelerate the leaching of both basic (eg Ca²⁺, Mg²⁺, K⁺, Na⁺) and acidic (Alⁿ⁺, H⁺) cations. The loss of base cations, especially Ca²⁺ and Mg²⁺, is of

special importance to sugar maple because it performs poorly on base-poor sites. The depletion of base cations from soils may reduce both the vigor of adult trees (Horsley *et al.* 2000) and the growth and survival of saplings (Kobe 1996; Kobe *et al.* 2002). Although sulfate concentrations in soils and drainage waters have decreased in the past few decades due to lower sulfur emissions mandated by the US Clean Air Act, the emissions and deposition of N have not declined (Driscoll *et al.* 2001). Sugar maple stands may be particularly sensitive to N deposition because of their propensity to produce the highly mobile nitrate ion, and the high sensitivity of this nitrification process to increased N accumulation in the soil (Lovett and Rueth 1999; Aber *et al.* 2003). Reported declines in sugar maple on unglaciated sites in northwestern and north-central Pennsylvania have been tentatively attributed to an interaction of base cation nutrition with stresses such as insect defoliation (Horsley *et al.* 2002). Declining sugar maple stands on the Allegheny plateau are associated with soils of low base cation availability (Bailey *et al.* in press). These stands showed marked improvement after liming (Long *et al.* 1997), which also suggests that low base cation status or low soil pH were involved in the decline of these trees. Although Allen *et al.* (1999) did not find a statistically significant relationship between acid deposition and sugar maple mortality at the regional scale, the unusually high mortality of sugar maple in Pennsylvania, an area of high acid deposition, warrants concern and further investigation (Driscoll *et al.* 2001).

Another factor potentially affecting sugar maple is climate change resulting from greenhouse gas emissions, which may alter the tree's range by reducing its competitive ability in the southern part of its range (Iverson and Prasad 1998). Predictions of vegetation patterns for climate scenarios in which atmospheric CO₂ concentrations are doubled indicate that suitable habitat for sugar maple will decline in the US, especially under the warmer, dryer conditions predicted by the Canadian Climate Center (CCC) model (Figure 5). The modeling approach illustrated in Figure 5 predicts species distributions after they have come into equilibrium in a stable climate, and ignores transitional periods in which species may persist outside their normal climatic range. Nonetheless, this exercise illustrates the potentially important effects of climate change on spatial distributions of tree species. It is also worth noting that Iverson and Prasad's (2001) predictions indicate that over most of its current range, the decline of sugar maple-dominated forest will be accompanied by an increase in oak-hickory forest, which would have a radically different effect on nitrogen cycling and retention (Lovett *et al.* 2002; Lovett *et al.* in press).

The Asian long-horned beetle (*Anoplophora glabripennis*), an introduced insect pest that feeds on maples, is another potential source of stress on sugar maple populations (USDA 1999). This insect was introduced to North America within the past decade, apparently in raw wood packing material from Asia (Milius 1999), and to date

there have been outbreaks in the vicinity of New York City, New Jersey, Chicago and Toronto. While this beetle can feed on several different hardwood trees, it appears to prefer maples, including sugar maple. It bores large holes in the trunks of trees, and the cumulative effect of these holes may eventually kill the tree. This insect could pose a serious threat to sugar maple if it spreads throughout the tree's range. Introduced pests and pathogens have the potential to nearly eliminate host trees, because the hosts often have little evolved resistance and the pest usually has no natural enemies. Good examples of this phenomenon in the 20th century include the chestnut blight, which has nearly wiped out the formerly dominant American chestnut (*Castanea dentata*) from its range, and Dutch elm disease, which has similarly devastated populations of American elm (*Ulmus americana*) (Campbell and Schlarbaum 2002). The Asian long-horned beetle has the potential to produce a swift and drastic decline in North American populations of sugar maple.

We predict that a substantial change in the abundance of sugar maple, for whatever reason, would produce a significant shift in N cycling in the forests of eastern North America. If sugar maple populations increase as a result of decreased competition from beech and hemlock, we expect that N leaching to surface waters will increase and N retention in forested watersheds will decrease in the affected areas. On the other hand, if sugar maple abundance declines because of any of the stresses discussed above (or for other reasons), a decline in nitrate leaching will follow, since replacement species will probably lower rates of nitrification in forest soils. This change in species composition could lead to less N leaching into drainage waters and greater N retention in soils. We believe the effect on N leaching could be large, given that species composition appears to be at least partially responsible for the roughly 20-fold variation in nitrate leaching among sites in the Catskill and Adirondack forests (Figure 4; Lovett *et al.* 2002; Mitchell *et al.* 2003). Changes in nitrate leaching could have important effects on surface water acidification and coastal zone eutrophication (Driscoll *et al.* 2003). Other possible consequences of changes in sugar maple populations include effects on wildlife habitat, forest aesthetics, and the timber and maple sugaring industries. Given the multiple environmental changes that may occur simultaneously in the next few decades, and the uncertainty in forecasting these changes, it is hard to predict the future of the sugar maple populations in North America. However, it is clear that perturbations of forest community composition, especially to a prominent and unique species such as sugar maple, could have widespread consequences for forest ecosystem function.

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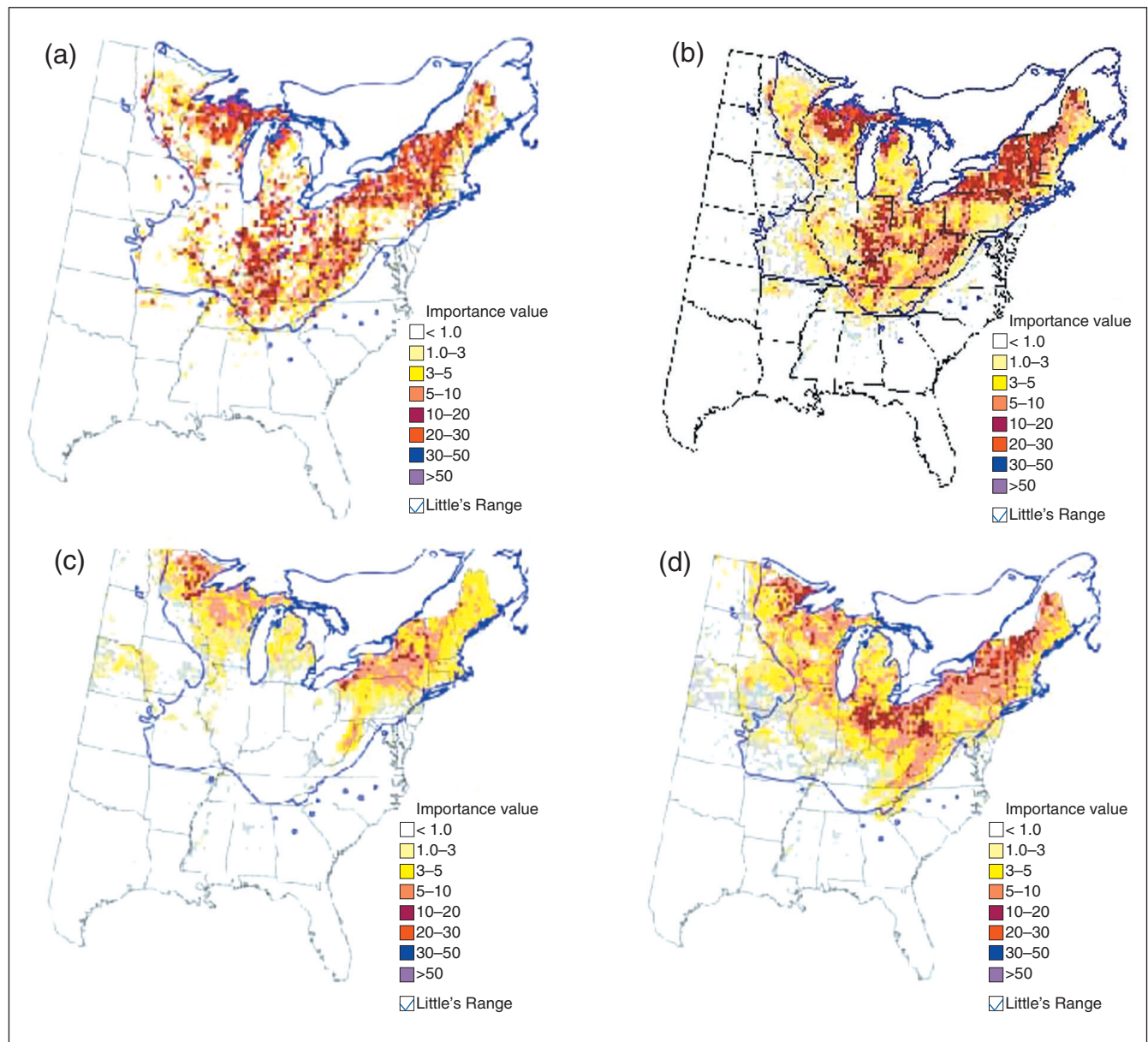


Figure 5. Current and predicted distributions of sugar maple importance value in the eastern US. (a) Observed distribution of sugar maple importance value derived from the data of the Forest Inventory and Analysis (FIA) program of the USDA Forest Service. (b) Importance value of sugar maple predicted by the DISTRIB modeling of Iverson and Prasad (2001) updated with finer spatial resolution and improved statistical techniques (A Prasad and L Iverson, pers comm). The model predicts sugar maple distribution and abundance based on climatic and physiographic factors. (c) and (d) Predicted suitable habitat and importance value based on the same model, but using a doubled- CO_2 climate scenario as predicted by the Canadian Climate Center global circulation model (c) and the Hadley global circulation model (d). “Little’s boundary” refers to the range maps published by Little (1971). Note that (a) represents actual occurrence of sugar maple, while (b), (c), and (d) represent predicted suitable habitat based on current (b) and future (c and d) climates. Unpublished data provided by A Prasad and L Iverson, USDA Forest Service. An older version of these simulations can be found in a paper by those authors on the Website www.fs.fed.us/ne/delaware/atlas/index.html.

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