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Nitrogen cycling, forest canopy reflectance, and emergent properties of ecosystems

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In Ollinger et al. (1), we reported that mass-based concentrations of nitrogen in forest canopies (%N) are positively associated with whole-canopy photosynthetic capacity and canopy shortwave albedo in temperate and boreal forests, the latter result stemming from a positive correlation between %N and canopy near infrared (NIR) reflectance. This finding is intriguing because a functional link between %N and NIR reflectance could indicate an influence of nitrogen cycling on surface energy exchange, and could provide a means for estimating %N using broad-band satellite sensors.

Recently, Knyazikhin et al. (2) dismissed our findings as counterintuitive and criticized subsequent studies (3, 4) for not considering physical mechanisms through which plants interact with light. Using a subset of data from ref. 1, Knyazikhin et al. (2) concluded that the %N-NIR relationship resulted from a spurious correlation between %N and structural properties that influence NIR scattering and are attributable to differences between conifer and broadleaf species. The authors reasoned that the lack of a direct biochemical mechanism means that NIR reflectance contains no useful information about canopy nitrogen, and that there can be no link between nitrogen, albedo, and climate. We argue that, quite to the contrary, the set of complex linkages between leaf, canopy, tree, and ecosystem properties that lead to repeatable correlations between mean %N and NIR reflectance represents a useful diagnostic tool, as well as an emergent property of ecosystems that has adaptive evolutionary origins.

We commend Knyazikhin et al. (2) for examining physical mechanisms influencing the %N-NIR relationship. However, their arguments rely on an assumption that a useful link between nitrogen and reflectance requires a direct, biochemical mechanism. Such a mechanism would indeed be counterintuitive because nitrogen-containing compounds absorb, rather than reflect, and typically influence narrow spectral features rather than broad spectral regions. Instead, our primary hypotheses involved functional associations between %N and structural

traits known to influence NIR scattering and reflectance. Our early ideas focused on anatomical leaf traits and were based on the fact that high rates of photosynthesis require both high %N and internal leaf structures that permit rapid CO₂ diffusion to chloroplasts. Our subsequent measurements failed to find a correlation between leaf %N and enhanced NIR scattering, and instead pointed to structural traits at the stem or canopy scale (3, 5). However, in all cases, our focus has been on functional associations between %N and plant structures rather than on direct effects of nitrogen itself.

As Knyazikhin et al. (2) note, the abundance of broadleaf and conifer species strongly affects reflectance patterns in mixed-species stands. However, composition alone cannot explain all variability in NIR reflectance. In our full dataset, which contains a greater number of pure broadleaf and pure conifer stands than the data considered by Knyazikhin et al. (2), the %N-NIR relationship was significant within as well as across forest types, and was also significant across multiple biomes when nonforest vegetation types were included. Even where mixed stands dominate, quantifying subpixel variation in forest composition is far from trivial and the ability to estimate whole-canopy %N has many useful applications, even where species composition is an important driver.

By arguing that the %N-NIR relationship is spurious, Knyazikhin et al. (2) effectively assume that a highly significant relationship that emerged from a large number of careful measurements was a coincidence. A more likely explanation stems from the fact that nitrogen availability is a primary constraint on carbon assimilation and, thereby, has a strong influence on multiple plant and canopy traits, including leaf morphology, leaf distribution, leaf orientation, proportional allocation to leaves versus wood, stem geometry, lateral branching, canopy height, and forest community composition (nitrogen availability is widely known to influence the abundance of broadleaf versus conifer species). The literature contains countless examples of these associations

(3), and an influence of altered nitrogen cycling on NIR reflectance via any of them cannot be discounted.

Identifying physical drivers of canopy NIR albedo is necessary, and modeling photon scattering in a canopy (2) can play a useful role. However, these physical mechanisms operate within a set of ecologically driven linkages between leaf, canopy, tree, and ecosystem properties, the prediction of which would represent a major step in understanding the role of nitrogen in the Earth system.

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