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Plant-soil stoichiometric changes along the succession from subalpine grasslands to shrublands in the Pyrenees

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The encroachment of shrub species into grasslands causes important changes at landscape and regional scale in many grass-dominated ecosystems from low to high latitudes. The expansion of shrubs is mostly caused by changes in climatic conditions and/or in land use. Shrub expansion is currently observed over a large proportion of alpine and subalpine grasslands across Europe and is expected to cause marked changes in ecosystem functioning. Some studies have reported that shrub encroachment favor an increase in the carbon (C) and nitrogen (N) content in the soil, and a decrease in soil pH, but such trends are expected to strongly depend on shrub characteristics and ecosystem features. Shrub and grass species belong to contrasting growth forms and differ in many functional traits related to their adaptive and reproductive capacity, and to their resources acquisition and allocation strategies. Therefore, the succession from grassland to shrubland is expected to cause important changes in the distribution, cycling, and stoichiometry of nutrients in the aboveground biomass and in the soil. In this study, we investigate the stoichiometric changes of the main grasses and shrubs involved in the succession from grasslands to shrublands in the northern and southern face of the Central Pyrenees. We analyzed the chemical composition in the soil and in different plant compartments in grasses and shrubs along the succession: in pure grasslands (initial stage), in mixed, young shrublands, and in mature, monodominant shrublands (final stage). The chemical composition of leaves, litter, and soil varied greatly between grasses and shrubs, and showed marked stoichiometric differences along the succession. Leaves of plant species occurring in the young and mature shrublands showed higher C and lower N and K concentrations compared to those in the pure grasslands. The C:P and the C:N ratios in soil increased along the succession in the northern and southern site respectively. Generally, shrub encroachment reduced the availability of nutrients in the soil and caused a lignification of aerial biomass. Some shrubs stored high amounts of nutrients in woody stems. Our results suggest that the encroachment of shrubs into subalpine ecosystems causes marked stoichiometric changes on the ecosystem and that these changes are strongly shaped by the functional differences between shrubs.