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Controls of Carrying Capacity: Degradation, Primary Production, and Forage Quality Effects in a Patagonian Steppe☆

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ABSTRACT

Rangeland carrying capacity depends on aboveground net primary production (ANPP) and on the sustainable harvest index (HIsust), the portion of ANPP that livestock can consume without undermining the production capacity of the system. At a regional scale, the observed harvest index (HIreal) increases with ANPP, but at a landscape scale the pattern is less clear, and controls of HIreal and HIsust are unknown. We analyzed the landscape patterns of variation of HIreal and HIsust across gradients of ANPP, pastoral value of vegetation (PV), and degradation. In 15 plots of a 2 753-ha paddock in a western Patagonian grass–shrub steppe, we estimated ANPP, consumption, forage pastoral value, and degradation. To estimate degradation we used PV weighed by forage cover because it was negatively correlated with a combination of ecosystem traits formerly linked to grazing-induced degradation. We calculated HIreal (consumption/ANPP) and HIsust (consumption removing 40% of aerial biomass of the key species/ANPP). We choose *Festuca pallescens* as the key species because of its high abundance and moderate preference. As the paddock was grazed with low stocking rate to maximize among-plots selection, HIreal was lower than HIsust. As in regional models, HIsust and HIreal increased with ANPP within the paddock ($R^2 = 0.33$ and 0.30, respectively). Multiple regressions showed that HIreal increased with ANPP and degradation, while HIsust increased with ANPP but decreased with degradation ($R^2 = 0.64$ and 0.77, respectively). This suggests that at stocking rates lower than carrying capacity, sheep choose highly productive stands and, at a given level of ANPP, they prefer degraded stands. In contrast, carrying capacity increases with productivity and decreases with degradation. Management systems based on HIsust may result in severe biomass removal of species more preferred than the key species *(Poa ligularis)*, and it is necessary to include strategies to preserve their individuals and populations.

Introduction

Estimating carrying capacity is a prerequisite for designing sustainable management systems of natural grasslands. Livestock carrying capacity is the animal density that an area can sustain without degrading forage resources and maintaining a level of secondary production coherent with landowner objectives and available management options (Holechek et al., 1989; Scarnecchia, 1990; Golluscio, 2009; Golluscio et al., 2009). Livestock carrying capacity can be estimated as the ratio between the amount of forage that can be sustainably consumed and the amount of forage that each individual animal must consume during a given period to attain the prefixed objectives of secondary production (Johnston et al., 1996). On the basis of the model of energy flux across the ecosystem (Odum, 1972), the forage that can be sustainably consumed is a fraction of aboveground net primary production (ANPP) beyond which plant productivity, energy supply to decomposers, integrity of nutrient cycles, and floristic composition are degraded (Golluscio, 2009).

Livestock carrying capacity is highly variable among years because of the high interannual variability of precipitation. As this variability is higher in arid than in humid zones (Paruelo and Lauenroth, 1998), it even questions the concept of carrying capacity in certain African ecosystems (Ellis and Swift, 1988). In addition, livestock carrying capacity depends on grazing management, which in turn can increase (e.g., McNaughton, 1985) or decrease ANPP (Milton et al., 1994). Finally, both forage resources and animal behavior are highly variable at different spatial scales, from region, to landscape, to community, to paddock (Senft et al., 1987). Within this conceptual framework, only long-term average carrying capacity may be roughly estimated on the basis of ANPP, individual animal consumption, and the proportion of ANPP that can be sustainably consumed. Here, this is called the

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sustainable harvest index (HIsust; Eq. (1)), also known as "safe" level of forage utilization (Johnston et al., 1996).

$$CC = ANPP \times HIsust \times IAC^{-1} \quad (1)$$

Where:

CC = Carrying capacity for livestock production ($animals \cdot ha^{-1}$)
ANPP = Aboveground net primary production ($kgDM \cdot ha^{-1} \cdot year^{-1}$)
HIsust = Harvest index sustainable for both ecosystem functioning preservation, and animal production under man-defined production objectives ($kgDM \cdot kgDM^{-1}$)
IAC = Individual annual consumption required as a function of the man-defined production objectives ($kgDM \cdot animal^{-1} \cdot year^{-1}$)

ANPP depends mainly on environmental factors, and IAC depends mainly on animal traits. Instead, the estimation of HIsust is a key component of carrying capacity assessment because it defines the real harvest index (HIreal) to be used, the variable most sensitive to human manipulation of rangelands (Golluscio et al., 1998a, 2009; Golluscio, 2009). As a consequence, it is essential to know the controls of HIsust at regional, landscape, and community scales. The regional scale allows quantifying the energy flux for broad ecosystem types and may be critical for government decisions (Oesterheld et al., 1992), while landscape and community scales are crucial in terms of ranch management (Senft et al., 1987; Golluscio et al., 1998a).

For South American rangelands most available information refers to HIreal (HIreal = observed consumption/ANPP), which does not necessarily coincide with HIsust. In addition, the patterns differ between spatial scales. At a regional scale, the main control of HIreal is ANPP, as shown by the direct relationship between HI and $ANPP^{0.5}$ derived by Golluscio et al. (1998a) from the double-logarithmic relationship between herbivore biomass and ANPP, obtained by Oesterheld et al. (1992). Thus, at a regional scale, livestock stocking rate increased in correspondence with a simultaneous increase of both ANPP and HIreal. However, when analyzing the same relationship for the subset of data corresponding to Patagonian steppes (ANPP < 1 500 $kgDM \cdot ha^{-1} \cdot y^{-1}$), HIreal decreased rather than increased with ANPP (Golluscio, 2009). This suggests that, at these community and landscape scales, controls other than ANPP would affect HIreal, even linked to environment (cold, snow, drinking water availability, predators, etc.) or to human management (real stocking rate, temporal use of forage resources, etc.).

The concept of Use Factor could aid to estimate HIsust. The Use Factor (Holechek et al., 1989) is the proportion of forage biomass of the "key species" that can be consumed by livestock without affecting plant production or floristic composition across time. The "key species," in turn, is that which can be used to estimate grassland trend and condition, mainly because of its moderate preference and/or abundance (Stoddart and Smith 1955). For North American grasslands similar to those of Patagonia, Holechek et al. (1989) proposed an empirical Use Factor of 50% to 30%, decreasing according to the ecological fragility of sites. In this paper we calculated HIsust by adding to measured animal consumption the biomass of the key species that would have been consumed under a Use Factor of 40%.

HIsust may be affected by ecosystem degradation induced by grazing because it often reduces ANPP and forage quality. The relatively common reduction of ANPP (Moen and Oksanen, 1998; Oksanen and Oksanen, 2000) and forage value of plant communities (Hofmann, 1989; Clauss and Lechner-Doll, 2001; Clauss et al., 2002) induces a reduction of carrying capacity, which commonly is not accompanied by a reduction of stocking rate, leading to a positive feedback that exacerbates the negative effect of grazing on the ecosystem (Le Houerou, 1977; Fisher and Turner, 1978; Dregne, 1983; Dodd, 1994; Prince et al., 1998). However, in certain cases, ANPP or forage quality may not be reduced under poor grazing management because preferred species may be replaced by other highly productive species, such as prostrate herbaceous species (Altesor et al., 2005) or shrub species (Archer, 1995; Aguiar et al., 1996). Additionally, grazing may favor certain highly palatable species that were subordinate to other less palatable but more aggressive species (Cingolani et al., 2005).

The Patagonian grass–shrub steppe dominated by *Festuca pallescens* is a good case study to analyze the controls of harvest index. First, it is one of the most productive communities of the Patagonian Phytogeographic Province (Paruelo et al., 2004). Second, it is one of the most studied communities in terms of carrying capacity, and both ANPP and forage quality have been included in local models to estimate carrying capacity of these steppes (Nakamatsu et al., 1998; Golluscio et al., 1998a; Elissalde et al., 2002; Golluscio et al., 2009; Golluscio, 2009). Third, several indicators of grazing-induced degradation have been identified for this community. From a physiognomic point of view, degradation was associated with a reduction of total cover and grass cover, as well as an increase of cover of litter, erosion pavements, and shrubs (Soriano and Brun, 1973; León and Aguiar, 1985; Perelman et al., 1997; Bertiller and Bisigato, 1998; Cesa and Paruelo, 2011). From a floristic point of view, degradation was associated to a reduction of the cover of several preferred grass species, such as *Bromus pictus, Poa ligularis, Festuca pallescens,* and *Pappostipa speciosa* (León and Aguiar, 1985; Cesa and Paruelo, 2011), and an increase in the cover of unpreferred grasses, such as *Pappostipa major,* and unpreferred shrubs and subshrubs, such as *Senecio filaginoides* (Soriano, 1956; León and Aguiar, 1985), *Mulinum spinosum* (León and Aguiar, 1985), and *Acaena splendens* (Cesa and Paruelo, 2011).

Our objective was to analyze the within-paddock patterns of HIreal and HIsust and relate them to ANPP, degradation, and forage quality. Under the hypothesis that forage availability will increase as ANPP and forage quality increase and degradation decreases, we predicted that in stands located within the same paddock and landscape unit, and dominated by the same set of species, both HIreal and HIsust would be positively related to ANPP and forage quality and negatively related to degradation. We tested this prediction by simple and multiple regressions on information obtained from a mensurative experiment done in 15 plots located within a paddock under controlled grazing. On each plot we measured consumption, ANPP, forage value of vegetation, and several degradation indicators. In order to estimate HIsust we first calibrated a nondestructive method to calculate the proportion of biomass removed from a visual scale of defoliation for the three most conspicuous species in the diet and then determined the key species on the basis of their abundance in the community and their preference by sheep.

Materials and Methods

Study Site

The work was done in the NW Chubut Province (Center West of Patagonia), a region with dissected relief and aridisol soils (Del Valle, 1998). Climate is cold-temperate, with mean temperatures from 4°C in July to 16°C in January and intense Western winds. Annual precipitation varies from 150 to 300 mm from West to East and is concentrated in winter. Precipitation is much lower than annual potential evapotranspiration (~600 mm, concentrated in summer), leading to a water balance with marked summer deficit and winter excess (Paruelo et al., 1998). The most conspicuous plant communities are the grass-shrub steppes of *Festuca pallescens, Pappostipa speciosa, Poa ligularis,* and *Mulinum spinosum* and the shrub-grass steppes of *Mulinum spinosum, Senecio* spp., *Pappostipa speciosa,* and *Poa lanuginosa* (León et al., 1998; Paruelo et al., 2004). Prairies are located following the drainage network, dominated by *Juncus balticus, Poa pratensis,* and *Festuca pallescens* ("sweet" mallines) or by *Distichlis* spp., *Juncus balticus,* and *Festuca pallescens* ("salt" mallines), the last ones more frequent toward the eastern region (Paruelo et al., 2004).

Experimental Layout

The experiment was done in fifteen 30 × 30 m plots located in grass–shrub steppe stands within the "Nevado" paddock (2 753 ha; estimated

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