

1 **Embracing a dynamic view of “pristine” seagrass meadows in the wake of**
2 **successful green turtle conservation**

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23 **Abstract**

24 What was “pristine” in the coastal oceans? The idea that climax vegetations represent a more
25 natural past is increasingly being called into question. Thanks to concerted conservation

26 efforts, recent decades have seen a remarkable recovery of multiple green turtle (*Chelonia*
27 *mydas*) populations in the world's oceans. These returning populations feed on tropical
28 seagrasses and radically transform meadows from continuous stretches dominated by climax
29 species to patchy multi-species complexes that change in space and time. A dynamic
30 spectrum of ecosystem states should replace climax meadows as reference states in
31 management plans, thus acknowledging risks of meadow collapse and enabling their
32 management.

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34 **Main Text**

35 An idealised conception of the pristine pervades ecological and conservation thinking, and is
36 typically influenced by a forest-centred view of nature ¹. The (mis-)conception of forests as
37 “pristine” state and savannahs as “degraded” has a marine equivalent in seagrass meadows.
38 Meadows composed of large, slow growing climax seagrass species are considered healthy,
39 while meadows with fast-growing pioneer seagrass species are considered disturbed or in
40 decline. This view inadvertently neglects the role that megaherbivore grazing played in the
41 past ¹ and reflects a much more recent functioning of seagrass meadows, long after their
42 principal megaherbivores (turtles and sirenians) became ecologically extinct ². Here we
43 document the dynamic stages meadows undergo as a result of megaherbivore-seagrass
44 interactions and propose them as a novel baseline against which to evaluate effective
45 management.

46 Recently, green turtles (*Chelonia mydas*), the large-bodied marine herbivores that feed on
47 seagrass, have seen significant population increases following centuries of low abundance.
48 This has resulted in locally dense aggregations of green turtles in their seagrass foraging
49 grounds. Their dramatic impact on seagrass seascapes is evidenced at five green turtle feeding
50 grounds in the Indian Ocean, Pacific Ocean, Atlantic Ocean and the Caribbean and is

51 schematized in Fig.1. At low turtle densities, green turtles feed on competitively dominant,
52 long-lived seagrass, selectively foraging on nutritious young leaf tissue. As grazing increases,
53 turtles create specific grazed areas within the meadow that they revisit and repeatedly graze,
54 maintaining high nutrient intake (described as ‘rotational grazing’³). Grazing increases plant
55 nutrient content⁴, and although productivity may initially increase⁵ it declines when grazing
56 intensifies and/or prolongs^{3,5}. Upon sustained grazing, rotational grazing shifts towards
57 random grazing while seagrass pioneer species gradually replace climax species^{3,6}.
58 Ultimately, pioneer shoot densities will decrease too, and turtles resort to digging up
59 rhizomes, targeting nutritious below-ground tissues⁵. This eventually leads to meadow
60 collapse, triggering turtle migrations to new foraging grounds. In some cases, meadow
61 collapse can occur even before turtles dig up the rhizome, when consumption far outweighs
62 productivity and pioneer species do not occupy the grazed areas⁴. These case studies show
63 that green turtles respond to changes in seagrass composition and abundance with
64 extraordinary flexibility in feeding strategies that allow them to exploit new meadow
65 resources while maintaining site-fidelity⁷.

66 The idea of large uninterrupted stands of climax ecosystems may be a much more recent
67 characterisation of ‘the pristine’, born of the extirpation of megaherbivores on land and in the
68 sea². Our case studies paint rather a different picture of the normal functioning of tropical
69 seagrass ecosystems. Our results suggest that ‘pristine’ seagrass meadows, with their full
70 complement of meso and mega herbivores, consist of spatio-temporally dynamic mosaics in
71 different states of grazing pressure and recovery. Meadows dominated by highly-grazed,
72 short-lived, pioneer species may exist cheek-by-jowl with meadows of long-lived climax
73 assemblages that have escaped grazing. We currently value seagrass meadows for the
74 numerous ecosystem services they provide, such as coastal protection, provision of habitat,
75 nutrient cycling and carbon storage. Though some of these services might be unaffected under

76 low herbivory⁸, and may be even enhanced under intermediate grazing, they are likely to be
77 significantly compromised when seagrass meadows become functionally extinct due to
78 intensified turtle grazing⁹. At seascape scale, in parallel with forest-savanna mosaics, a full
79 spectrum of seagrass meadow states likely provides a higher diversity of ecosystem services
80 than a sea fringed solely by long-lived climax meadows.

81 How do we reconcile this new dynamic baseline with the conservation of seagrass meadows
82 and their functioning? For a start, it requires us to move beyond polarised conservation
83 approaches that privilege either turtle numbers or seagrass meadow functions. It may be
84 critical to accept that seagrass mosaics, characterised by a full spectrum of meadow states,
85 from rich, fully developed meadows to sparse habitats, are not signs of a degraded seascape
86 and, in fact, may reflect pre-Anthropocene ecosystems more closely. By embracing this much
87 more nuanced understanding we move from the view of “nature in balance” that still pervades
88 literature and environmental policy¹, towards embracing the “flux of nature”, where
89 herbivory (and disturbances, in general) plays a central role. Increasing green turtle
90 populations may lead to seagrass meadows that cycle through periods of decline and recovery
91 worldwide. However, recovery of seagrass beds ‘from scratch’ is typically slow and
92 unpredictable¹⁰. Borrowing from forest-savannah systems, this state would be the equivalent
93 of a terrestrial ‘desert’. It may be necessary to intervene in grazed meadows before imminent
94 collapse. Measures could be taken to exclude turtles, either from small remnant patches to
95 facilitate meadow recovery once turtles have abandoned the site or to exclude grazing for
96 example through(re-)introduction of calcareous free-living algae that protect basal leaf
97 sections, meristems and roots¹¹. These ameliorative measures take on even more urgency as
98 seagrass habitat degradation intensifies due to human influence. In light of the degrading state
99 of tropical seagrass meadows we may also need to revisit active green turtle conservation
100 efforts, involving stakeholders in both seagrass and sea turtle conservation.

101 Conceptions of the pristine are more value-laden rather than ecologically relevant. Rather
102 than attempting to manage for a “pristine” meadow in equilibrium state that might be largely
103 incompatible with abundant megaherbivores, we call for embracing a much more nuanced
104 management that include seascapes characterised by inherently non-equilibrium dynamics,
105 even if some of these habitats provide fewer ecosystem services. While green turtles represent
106 a rare conservation success at some locations, turtle populations continue to face a suite of
107 pressures worldwide. The dramatic ecosystem impacts turtles have at these few locations
108 should not compromise global conservation efforts. As conservation successes of ecosystem-
109 modifying flagships continue, we may need to acknowledge that the dynamic mosaics they
110 create, impoverished as some of them may seem, are paradoxically closer to pristine
111 conditions than our Edenic conceptions of them.

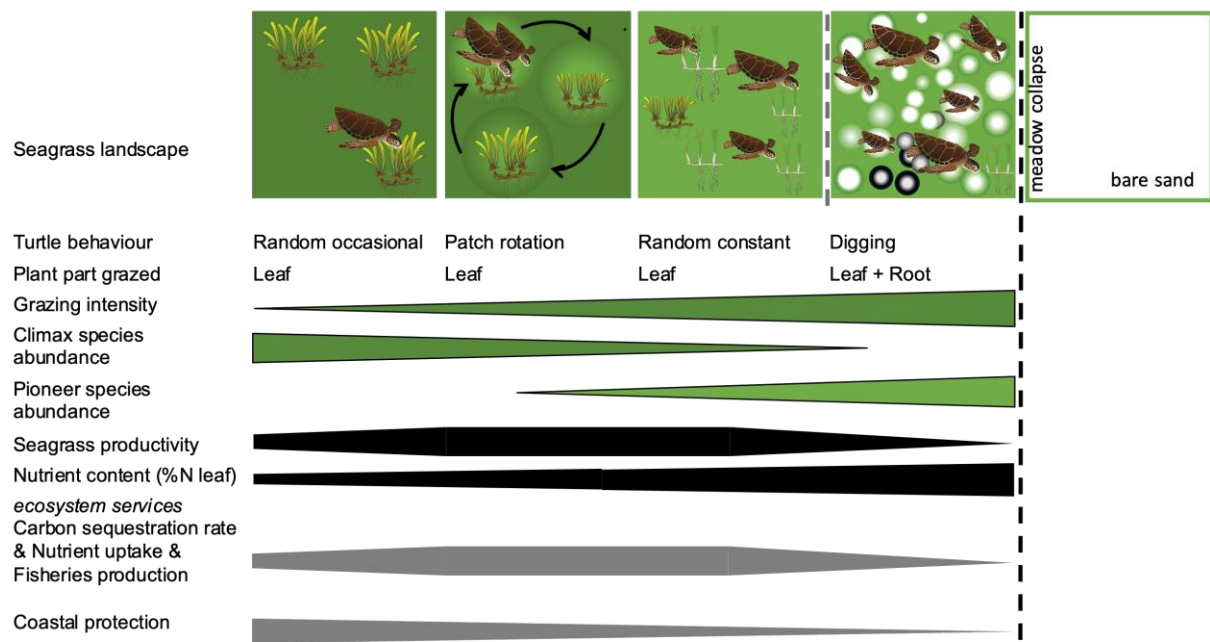
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Fig. 1. Green turtle grazing impact on seagrass seascapes. Under increased turtle densities (from left to right) and sustained turtle grazing regimes, turtles change feeding strategies to exploit new meadow resources while maintaining site fidelity. Seagrass meadows experience dramatic changes in their landscape features, nutrient quality, primary production, species composition and ecosystem services. Meadow collapse can either occur after intensive random leaf grazing in meadows where pioneer species are absent, depicted by the gray dashed line, or as a result of erosion following digging, depicted by the black dashed line. Estimated ecosystem services trends adapted from ⁹, carbon sequestration trends adapted from ¹².