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A Busse Balloon in the Lagoon: Herbivore Behaviour Generates Spatial Patterns in Coral Reef Ecosystems

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ABSTRACT

Spatial processes, particularly scale-dependent feedbacks, may play important and underappreciated roles in the dynamics of bistable ecosystems. For example, self-organised spatial patterns can allow for stable coexistence of alternative states outside regions of bistability, a phenomenon known as a Busse balloon. We used partial differential equations to explore the potential for such dynamics in coral reefs, focusing on how herbivore behaviour and mobility affect the stability of coral- and macroalgal-dominated states. Herbivore attraction to coral resulted in a Busse balloon that enhanced macroalgal resilience, with patterns persisting in regions of parameter space where nonspatial models predict uniform coral dominance. Thus, our work suggests herbivore association with coral (e.g., for shelter) can prevent reefs from reaching a fully coral-dominated state. More broadly, this study illustrates how consumer space use can prevent ecosystems from undergoing wholesale state transitions, highlighting the importance of explicitly accounting for space when studying bistable systems.

1 | Introduction

Ecologists have long been fascinated by the observation that seemingly identical environments can support dramatically different communities. Theory predicts this phenomenon can arise due to bistability, or the existence of alternative ecosystem states that are stable under the same environmental conditions (Beisner et al. 2003; Scheffer and Carpenter 2003). Alternative stable states have been documented in numerous ecosystems, including coral reefs, kelp forests, lakes and savannas (Schmitt et al. 2019; Ling et al. 2015; Scheffer et al. 1993; Staver et al. 2011). Bistability makes these systems challenging to manage due to the potential for abrupt transitions between states, and because reversing these transitions may require more than just restoring the environmental conditions that preceded them (hysteresis). Theoretical models have been integral to studies of such dynamics; however, most are nonspatial and predict wholesale transitions between states when parameters exceed tipping points or when perturbations move the system outside a state's basin of attraction (Beisner et al. 2003; Kéfi et al. 2022). In real ecosystems, processes maintaining alternative states operate over distinct spatial scales, and this scale-dependency may modulate state transitions. For example, if the strength of a positive feedback decreases with distance, a system can form self-organised Turing patterns (Turing 1952). If Turing patterns form and extend beyond tipping points ('Turing-before tipping'), the system can avoid a full transition to an alternative state, resulting in localised rather than widespread state shifts (Bastiaansen et al. 2018;

Rietkerk et al. 2021). The region of parameter space over which stable Turing patterns exist, the 'Busse balloon', therefore provides a measure of the resilience of ecosystem states in spatially extended bistable systems (Rietkerk et al. 2021).

Despite extensive research on alternative stable states, the potential for Busse balloon formation has not been widely explored in ecology. The best-studied examples are from savanna ecosystems, where there is evidence of self-organised mosaics of grassland and forest (Baudena and Rietkerk 2013; Aleman et al. 2020; Rietkerk et al. 2021). The extent to which similar dynamics occur in other bistable ecosystems remains uncertain. This gap includes coral reefs, which are incredibly productive and biodiverse but also highly threatened by climate change and local anthropogenic activities. Degraded reefs can transition from coral dominance to an alternative macroalgal-dominated state (Hughes et al. 2007; Schmitt et al. 2022) and numerous (largely nonspatial) 'coral-macroalgal-turf' models have been developed to study these state shifts (Mumby et al. 2007; Blackwood et al. 2018). This extensive theoretical foundation–along with the urgent need to conserve coral reefs and the societal benefits they provide–makes coral reefs an ideal system for investigating pattern formation.

The strength of grazing on macroalgae has a major effect on the stability of coral and macroalgal-dominated states (Cheal et al. 2010; Schmitt et al. 2019; Mumby et al. 2007). Herbivore space use, which determines spatial distributions of grazing pressure, could therefore be a key driver of coral-macroalgal dynamics. For example, models suggest localised grazing by spatially constrained herbivores is more effective at preventing macroalgal establishment than the diffuse grazing of highly mobile herbivores (Eynaud et al. 2016) and that more intense grazing in topographically complex areas of a reef can create positive feedbacks between the abundance of structure-providing corals and herbivores (Bozec et al. 2013). Unequal grazing pressure across a reefscape can arise from herbivore substrate preferences (Santano et al. 2021), and this heterogeneous grazing may have dramatic effects. For example, on the Great Barrier Reef, herbivores' strong association with reef structure has resulted in prominent grazing halos around patch reefs (Madin et al. 2011). Some herbivores also appear to avoid dense macroalgal stands, which may promote macroalgal dominance in these areas (Hoey and Bellwood 2011).

Although reef herbivores seem capable of generating spatial heterogeneity, this group displays an enormous amount of functional diversity that may mediate their effects on the benthos (Thibaut et al. 2012). The impacts of herbivore diversity on the stability of coral- and macroalgal-dominated states have been well studied, but most of this work has focused on herbivore diets (Green and Bellwood 2009; Burkepile and Hay 2008; Cook et al. 2024). The roles of movement-based functional groups have not been widely explored, despite herbivores exhibiting diverse foraging ranges and substrate preferences (Carpenter 1986; Nash et al. 2013; Chow et al. 2021). Theory predicts specific types of herbivore space use (e.g., selective foraging) promote pattern formation in grazed systems, whereas others (e.g., indiscriminate foraging) inhibit it (Ge and Liu 2021). Thus, the 'movement' functional diversity of reef herbivore communities–particularly the relative abundance of groups with 'pattern-forming' or 'pattern-inhibiting' traits–may have large consequences for benthic dynamics.

In this study, we built spatially explicit (partial differential equation) versions of existing coral–macroalgal–turf models and used them to investigate how herbivore space use influences the stability of coral- and macroalgal-dominated states on spatially extended reefs. Using fishing as our environmental parameter of interest (as overfishing of herbivores is a major threat to coral reefs worldwide; Hughes et al. 2003), we compared the equilibrium spatial distributions of coral and macroalgae predicted by each spatial model to the corresponding nonspatial model's equilibria across a range of fishing pressures. Our goal was to determine whether Busse balloons were possible in this system (i.e., whether coral and macroalgae could coexist in stable patterns outside the region of bistability). We explored how the existence and characteristics of these balloons varied with herbivore diffusion and strength of attraction to (or avoidance of) coral, and compared modelled and real fish movement trait distributions to understand the relative likelihood of pattern formation. This work provides further insight into the importance of herbivore space use for benthic dynamics on coral reefs and serves as a novel example of how nonspatial models' predictions of abrupt tipping between alternative states may not always hold in more realistic, spatial contexts.

2 | Methods

To model the dynamics of a spatially extended coral reef, we built a partial differential equation (PDE) model that incorporates key local dynamics (coral-macroalgal competition for benthic space, grazing on macroalgae) and spatial processes like herbivore movement. Unlike previous spatial coral-macroalgal-turf models, which generally consist of discrete patches connected by dispersal (Greiner et al. 2022; Rassweiler and Wall 2024), grids of neighbouring cells (Mumby et al. 2006; Eynaud et al. 2016), or incorporate empirical relationships between spatial features and herbivory (Bozec et al. 2013), PDE models treat space as a continuous independent variable. This not only allows PDEs to capture variation in benthic cover and grazing across a continuous range of spatial scales but also enables processes like movement to be made explicit functions of space, resulting in a more nuanced analysis of spatial dynamics than is possible with patch or grid-based models (Holmes et al. 1994; Meron 2012).

Following recent studies (Kopecky et al. 2023, Cook et al. 2024, Rassweiler and Wall 2024), we described local benthic dynamics using the model published by Briggs et al. (2018), but modified this model by adding dynamic herbivores and making it spatially explicit. The original Briggs model tracks the proportional cover of coral C, invulnerable macroalgae M_I and vulnerable macroalgae M_V (see Table 1 for all state variables and parameters). The proportion of space not occupied by these groups ($1\text{-}C\text{-}M_I\text{-}M_V$) is assumed to be occupied by turf algae T, which is functionally equivalent to empty space. Coral, invulnerable macroalgae and vulnerable macroalgae grow on turf at rates g_{TC}, g_{TI} and g_{TV}, respectively. Invulnerable macroalgae can overgrow coral at a rate γg_{TI}, where γ scales the rate of growth over coral relative to growth on turf. Vulnerable macroalgae, which represent early life stages with fewer defences (Davis 2018; Puk et al. 2020), are

TABLE 1 | Model state variables and parameters. To facilitate comparison with previous studies, nonspatial parameter values were taken from Briggs et al. (2018) where possible (with the exception of external recruitment and coral death rate, which were varied slightly to expand the range of fishing pressures where patterns occurred).

Symbol	Description	Units	Default value
State variable			
C	Coral cover	Prop.	—
M_I	Invulnerable macroalgal cover	Prop.	—
M_V	Vulnerable macroalgal cover	Prop.	—
H	Herbivore biomass	kg	—
t	Time	year	—
x	Space	m	—
Nonspatial parameters			
g_{TC}	Coral growth on turf	year^{-1}	0.1
φ_C	Coral external recruitment rate	year^{-1}	0.01
d_C	Coral mortality rate	year^{-1}	0.02
g_{TV}	Growth of vulnerable macroalgae on turf	year^{-1}	0.2
φ_M	Macroalgae external recruitment rate	year^{-1}	0.01
r_M	Production of vulnerable macroalgae from invulnerable macroalgae	year^{-1}	0.5
ω	Maturation rate of macroalgae from vulnerable to invulnerable stage	year^{-1}	2
g_{TI}	Growth of invulnerable macroalgae on turf	year^{-1}	0.4
γ	Growth of invulnerable macroalgae over coral relative to growth over turf	—	0.4
d_V	Vulnerable macroalgae mortality rate	$\text{year}^{-1}\,\text{kg H}^{-1}$	2
d_I	Invulnerable macroalgae mortality rate	$\text{year}^{-1}\,\text{kg H}^{-1}$	0.4
r_H	Herbivore growth rate	year^{-1}	0.2
d_H	Herbivore density-dependent mortality rate	$\text{kg H}^{-1}\,\text{year}^{-1}$	0.1
φ_H	Herbivore external recruitment rate	year^{-1}	0.05
f	Fishing pressure	year^{-1}	varied
Spatial parameters			
D_C	Coral diffusion rate	$\text{m}^2\,\text{year}^{-1}$	0.05
D_M	Macroalgae diffusion rate	$\text{m}^2\,\text{year}^{-1}$	0.05
D_H	Herbivore diffusion rate	$\text{m}^2\,\text{year}^{-1}$	0.25
τ_C	Herbivore taxis with respect to coral	$\text{m}^2\,\text{C}^{-1}\,\text{year}^{-1}$	−0.75

produced by invulnerable macroalgae at a rate r_M and mature into invulnerable macroalgae at a rate ω. Both coral and vulnerable macroalgal cover arise from external recruitment onto turf at rates φ_C and φ_M, respectively. Finally, coral experiences natural mortality at a rate d_C, and invulnerable and vulnerable macroalgae experience grazing mortality at rates d_I and d_V (which we modified to be per unit herbivore biomass, meaning total macroalgal mortality is $d_I H$ and $d_V H$). The nonspatial model predicts the benthic community will equilibrate in either a coral or macroalgal-dominated state, with potential for bistability of these states when $d_V > d_I$ (i.e., when macroalgae reach a size refuge from herbivory; Briggs et al. 2018).

Given the expected importance of the spatial distribution of grazing pressure for benthic dynamics, we modified the original Briggs model to explicitly track herbivore biomass dynamics. Similarly to previous models with dynamic herbivores (e.g., van de Leemput et al. 2016), we assumed herbivore biomass H is lost due to density-dependent mortality d_H and fishing pressure f and increases due to local growth r_H and external recruitment

φ_H (with φ_H representing recruitment of small juveniles, contributing relatively little to biomass growth). Our nonspatial (ordinary differential equation, ODE) model is therefore:

$$\frac{dC}{dt} = \varphi_C T + g_{TC}TC - \gamma g_{TI}M_I C - d_C C \tag{1}$$

$$\frac{dM_V}{dt} = \varphi_M T + r_M TM_I + g_{TV}TM_V - d_V HM_V - \omega M_V \tag{2}$$

$$\frac{dM_I}{dt} = \omega M_V + g_{TI}TM_I + \gamma g_{TI}M_I C - d_I HM_I \tag{3}$$

$$\frac{dH}{dt} = \varphi_H + r_H H - d_H H^2 - fH \tag{4}$$

Equations (1–4) describe community dynamics at a single spatial location. We used PDEs to extend this model to a continuous, one-dimensional landscape (Equations 5–8). We allowed coral, invulnerable macroalgae and herbivores to diffuse across this landscape with diffusion coefficients D_C, D_M and D_H, respectively. Diffusion of invulnerable macroalgae can be thought of as lateral growth into regions with lower cover, and coral diffusion as both lateral growth and localised dispersal and recruitment of larvae (similar to representations of diffusion in plants; HilleRisLambers et al. 2001, Marick et al. 2024). We ignored diffusion of vulnerable macroalgae, as this stage matures locally into invulnerable individuals (for simplicity we refer to diffusion of invulnerable macroalgae as macroalgal diffusion). We used Neumann (reflecting) boundary conditions in our simulations; to avoid edge effects, we only report metrics (spatial averages, pattern characteristics) from within the central 50% of the landscape.

Herbivore diffusion represents random movement of individuals, with higher values indicating greater mobility. We also allowed for behaviorally driven movement in the form of taxis with respect to coral (τ_C). Negative values of τ_C mean herbivores are attracted to coral (e.g., because it provides shelter) while positive values mean they avoid it (e.g., because areas with high coral cover offer less food than areas with abundant algae).

$$\frac{\partial C}{dt} = \varphi_C T + g_{TC}TC - \gamma g_{TI}M_I C - d_C C + D_C\frac{\partial^2 C}{\partial x^2} \tag{5}$$

$$\frac{\partial M_V}{\partial t} = \varphi_M T + r_M TM_I + g_{TV}TM_V - d_V HM_V - \omega M_V \tag{6}$$

$$\frac{\partial M_I}{\partial t} = \omega M_V + g_{TI}TM_I + \gamma g_{TI}M_I C - d_I HM_I + D_M\frac{\partial^2 M_I}{\partial x^2} \tag{7}$$

$$\frac{\partial H}{\partial t} = \varphi_H + r_H H - d_H H^2 - fH + D_H\frac{\partial^2 H}{\partial x^2} + \tau_C\frac{\partial}{\partial x}\left(H\frac{\partial C}{\partial x}\right) \tag{8}$$

We used the PDE model (Equations 5–8) to explore how herbivore diffusion (D_H) and behaviour (strength and direction of taxis in response to coral, τ_C) influence the stability of coral and macroalgal-dominated states at different fishing pressures. We were particularly interested in conditions that enable pattern formation and whether patterns occurred at fishing pressures outside the region of bistability. We therefore constructed bifurcation diagrams as a function of fishing pressure for both our ODE and PDE models, using the nonspatial (ODE) model equilibria as our baseline expectations for the stability of each state and comparing these to the spatial averages of the steady-state coral and macroalgal distributions predicted by the PDE. Our herbivore movement parameters do not have direct connections to common metrics of herbivore mobility, making empirical estimates challenging. Given the evidence for positive relationships between the abundance of common herbivores and reef structural complexity (e.g., coral height, number of corals, rugosity; Newman et al. 2015, Harborne et al. 2012, Graham and Nash 2013), we chose values of taxis and diffusion that produced attraction to coral ($\tau_C = -0.75\,\text{m}^2\,\text{C}^{-1}\,\text{year}^{-1}$, $D_H = 0.25\,\text{m}^2\,\text{year}^{-1}$) as our default herbivore traits. To account for uncertainty in these parameters, we explored a large range of values of both taxis and diffusion.

We initialized our simulations with spatially alternating coral and macroalgal patches represented by step functions, as this allowed us to easily vary initial landscape characteristics (e.g., patch widths, patch heights) to discern their effects on emergent patterns. An analysis of other initial conditions (sinusoidal and random; see the 'Model Initialization' section in Appendix S1 and Figures S6, S7) confirmed that this initialization produced spatial patterns that were representative of those emerging from a range of initial states. This analysis also revealed that the initial width of coral and macroalgal patches influenced pattern characteristics at lower fishing pressures, and we therefore considered several initial patch widths in our main text simulations. For simplicity, we initialized herbivores at their nonspatial equilibrium at all locations (but see Appendix S1 for heterogeneous initializations).

Having found that our default parameterisations produced patterns in benthic cover (alternating coral and macroalgal patches), we investigated the effects of herbivore diffusion and taxis on these patterns. To determine the region of taxis–diffusion trait space where patterns existed, we calculated the minimum strength of taxis towards coral required for pattern formation (at a fishing pressure just outside the region of bistability) as a function of herbivore diffusion rate. We then investigated how taxis and diffusion affected the range of fishing pressures over which patterns occurred and the characteristics of these patterns. We used several metrics to characterise spatial patterns: coral patch density (number of coral patches in middle 50% of the landscape), coral patch width (distance between the locations on either side of a coral patch where coral has fallen to half the maximum cover in the patch), maximum coral cover in a coral patch, and average coral cover across the middle 50% of the landscape. We repeated these analyses for two sets of initial conditions (a high number of narrow coral and macroalgal patches, each with a width of 1/64 the length of the landscape, or a landscape with two patches, one high-coral and one high-macroalgae, each with a width of ½ the length of the landscape).

To investigate the effects of community-level herbivore movement traits on spatial pattern formation, we modified our model to include two herbivore populations (equations 9–10). We assumed these populations (referred to as A and B) have identical growth rates, density-dependent mortality rates, and grazing rates but differ in movement traits (diffusion and taxis) and fishing pressure. We set the rates of external recruitment and density-dependent mortality in each population equal to one-half and twice the rates in the single population model, respectively.

$$\frac{\partial H_A}{\partial t} = \varphi_H / 2 + r_H H_A - 2d_H {H_A}^2 - f_A H_A + D_{HA}\frac{\partial^2 H_A}{\partial x^2} + \tau_{CA}\frac{\partial}{\partial x}\left(H_A \frac{\partial C}{\partial x}\right) \tag{9}$$

$$\frac{\partial H_B}{\partial t} = \varphi_H / 2 + r_H H_B - 2d_H {H_B}^2 - f_B H_B + D_{HB}\frac{\partial^2 H_B}{\partial x^2} + \tau_{CB}\frac{\partial}{\partial x}\left(H_B \frac{\partial C}{\partial x}\right) \tag{10}$$

By varying the relative fishing pressure on each population but holding total herbivore biomass constant, we were able to independently analyse the effects of herbivore community composition on pattern formation. We used the results of these analyses, together with a literature review of the movement traits of the herbivore community in Moorea[1], French Polynesia (which has intensively studied coral reefs with strong empirical evidence for coral-macroalgal bistability; Schmitt et al. 2019), to investigate whether observed heterogeneity in coral and macroalgal cover in Moorea's lagoons could be driven by herbivore space use.

To test the robustness of our results to the underlying nonspatial model, we repeated our analyses using two alternative models of local benthic dynamics: (1) the original coral–macroalgae–turf model introduced by Mumby et al. (2007) with the addition of external recruitment (Elmhirst et al. 2009), and (2) the external recruitment Mumby model with a Holling Type II grazing functional response (van de Leemput et al. 2016). These models, which are described in more detail in Appendix S1, differ from each other and from the Briggs model in the primary feedbacks that generate bistability. Thus, comparing these models allowed us to explore the sensitivity of spatial dynamics to the underlying mechanisms of bistability. We also explored the sensitivity of our results to herbivore growth and external recruitment, including scenarios in which total herbivore biomass was held constant (see Appendix S1). All simulations were performed in Matlab vR2023b.

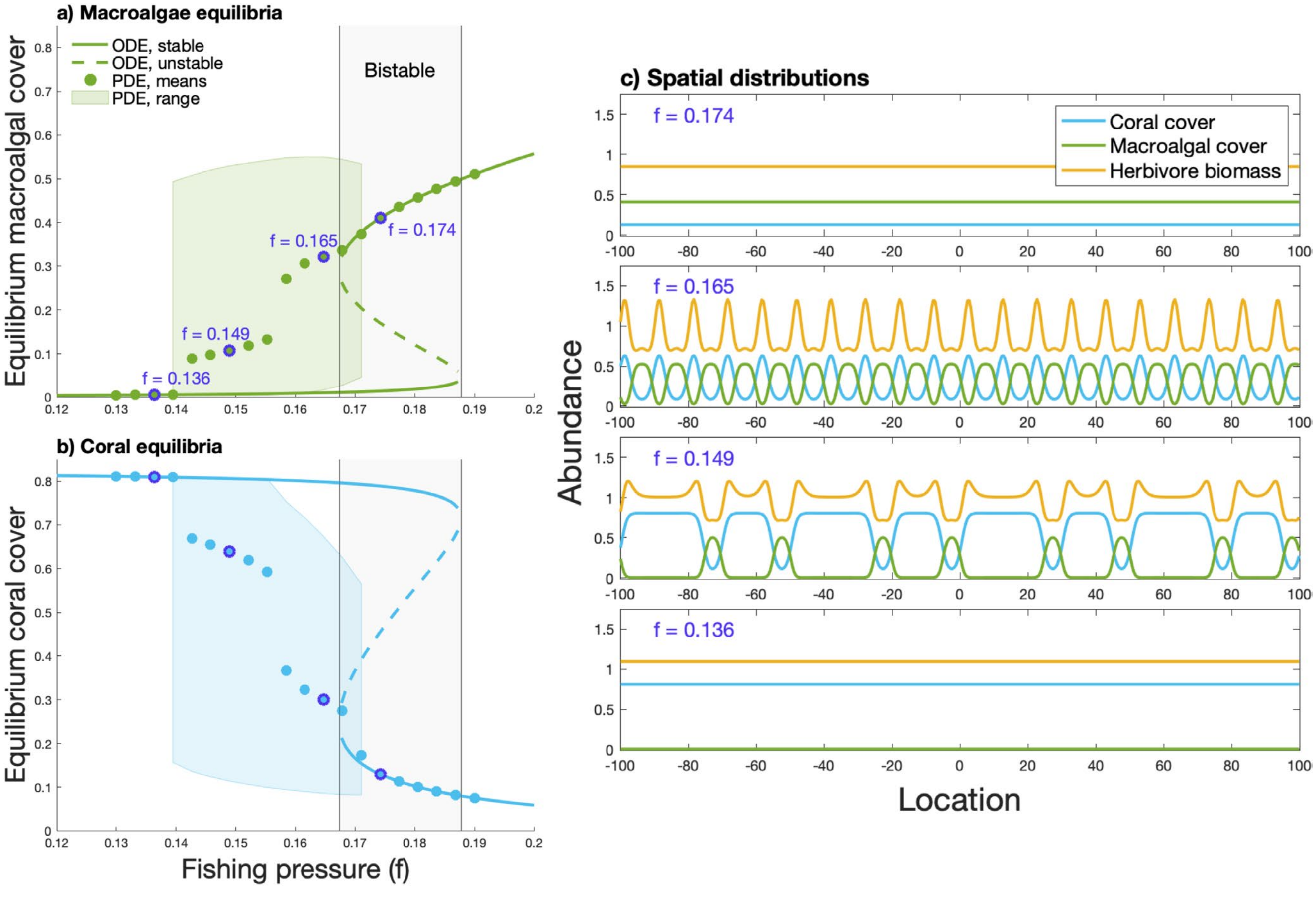

FIGURE 1 | Example of the Busse balloon formed by herbivore attraction to coral ($\tau_C = -0.75\,\mathrm{m}^2\,\mathrm{C}^{-1}\,\mathrm{year}^{-1}$, $D_H = 0.25\,\mathrm{m}^2\,\mathrm{year}^{-1}$). The bifurcation diagrams in (a) and (b) show the effect of fishing pressure f on equilibrium cover of macroalgae (a) and coral (b). Solid and dashed lines represent stable and unstable equilibria in the nonspatial (ODE) model, with the region of bistability shaded in grey. Points indicate the spatially averaged equilibrium cover predicted by the PDE model; the full spatial distributions of coral, macroalgae and herbivores at four fishing pressures (labelled in dark blue) are shown in (c). The spatial means and distributions are from simulations initialized with coral and macroalgal patch widths of 1/16 the length of the landscape. The green and blue shaded areas in (a) and (b) indicate the range between maximum and minimum macroalgal and coral cover (i.e., the cover at the peaks and troughs of the patterns) in the equilibrated landscape. These are composite envelopes showing the maxima and minima from across a range of initial conditions and thus indicate the highest and lowest cover of each group that could be expected in patterns within the balloon. Note that here and in all figures, macroalgal cover represents the sum of vulnerable and invulnerable macroalgal cover.

3 | Results

When herbivores had relatively low diffusion and moderate attraction to coral, the spatial model predicted the existence of a Busse balloon that extended from within the region of bistability to past the low-fishing (macroalgal to coral) tipping point (Figure 1a,b). In this Busse balloon, self-organised patterns allowed macroalgae to persist locally at fishing pressures for which the nonspatial model predicted complete coral dominance (Figure 1c). The characteristics of these patterns varied with fishing pressure (Figure 1c, Figure S1), resulting in gradual transitions between macroalgal and coral dominance as fishing pressure decreased. This spatial patterning thus increased the resilience of the macroalgal state, with resilience defined here as the magnitude of change in environmental conditions (fishing pressure) the system can tolerate without fully tipping between states. Patterns formed with even the slightest initial heterogeneity in benthic cover (e.g., 5% or 95% coral dominance), but only when herbivores were attracted to coral (Figure S2). Patterns did not form if herbivores ignored or avoided coral; furthermore, initially patchy landscapes tended to reach a homogeneous state more quickly when herbivores avoided coral than when they ignored it (Figure S3).

Patterns within the Busse balloon were dependent on initial conditions. Analysis of a wide range of initializations (see Appendix S1) suggested that landscapes with greater initial heterogeneity in coral cover are more prone to pattern formation, likely because these landscapes promote rapid establishment of variation in herbivore biomass that then leads to stable patterns in coral and macroalgal dominance (Figures S4–S8). When the landscape was initially homogeneous, there was generally no pattern formation (Figure S2). Initial condition dependence was strongest at lower fishing pressures (e.g., $f = 0.146\,\text{year}^{-1}$ in Figures S4–S8); here, high herbivore biomass meant macroalgae could only persist if the landscape produced sufficiently strong initial movement of herbivores away from macroalgal-dominated patches. Initial conditions were less important at higher fishing pressures near the tipping point (e.g., $f = 0.158\,\text{year}^{-1}$ in Figures S4–S6), where wide initial patches tended to split into smaller ones until a stable width was reached.

The Busse balloon was robust to local (+/−10%) variation in nonspatial parameters (Figure S9), although it was sensitive to external recruitment of coral and macroalgae (Figure S10). External coral recruitment was needed for a fully 'inflated' balloon in which average macroalgal cover did not collapse immediately after the tipping point. However, coral recruitment also shifted the balloon and region of bistability to higher fishing pressures and thus overall had a positive effect on coral (Figure S10). Due to our interest in exploring the maximum extent of the Busse

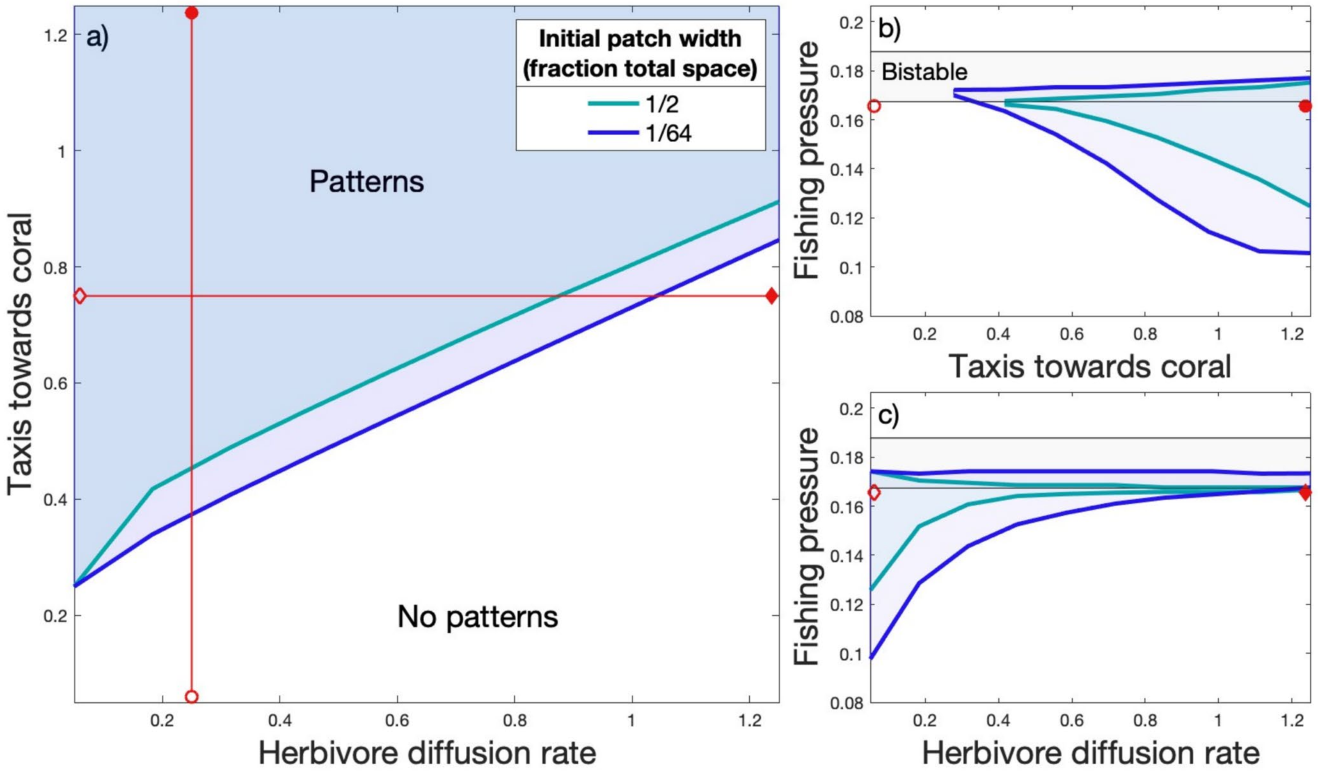

FIGURE 2 | Effect of herbivore diffusion and strength of taxis towards coral on the existence of patterns. (a) Operating diagram showing the combinations of herbivore diffusion and taxis over which patterns are possible for two sets of initial conditions (note since the y-axis is taxis towards coral, the true values of τ_C are negative). Fishing pressure was set to $0.1657\,\text{year}^{-1}$, which is just below the lower boundary of bistability, where the nonspatial model predicts only the coral-dominated state is stable. (b) and (c) show the effects of taxis and diffusion, respectively, on the range of fishing pressures over which patterns occur. The red vertical and horizontal lines indicate the sections of the operating diagram represented at the corresponding fishing pressures in (b) and (c), respectively, with open symbols (circles for taxis, diamonds for diffusion) at the starting points and closed symbols at the end points. For clarity the lines are not shown in (b, c).

balloon, we used higher values of external coral and macroalgal recruitment in our analyses than the default values used by Briggs et al. (2018), which also required decreasing the default coral mortality rate (from 0.05 to 0.02 year^{-1}) to maintain bistability. These changes had minimal qualitative effects on our findings (Figure S11). Reducing coral and macroalgal diffusion rates increased mean macroalgal cover within the balloon, but the effect of coral diffusion was much stronger (Figure S13). Regardless of coral and macroalgal diffusion rates, herbivore taxis towards coral was still needed for stable patterns– low coral or macroalgal diffusion alone was not sufficient for the persistence of initial patches (Figure S13).

The level of herbivore attraction to coral required for pattern formation increased with herbivore diffusion rate (Figure 2, Figure S14). Stronger taxis towards coral enabled patterns to persist over a larger range of fishing pressures, whereas stronger diffusion had the opposite effect (Figure 2, Figure S15). Patterns did not form when herbivores avoided coral, regardless of the strength of this avoidance (Figure S15a). As the strength of taxis towards coral increased, the density of coral patches increased; these patches were narrower and had lower maximum coral cover, and mean coral cover across the landscape decreased (Figure 3). Increasing herbivore diffusion had the opposite effect on patterns, promoting higher average coral cover (Figure 3).

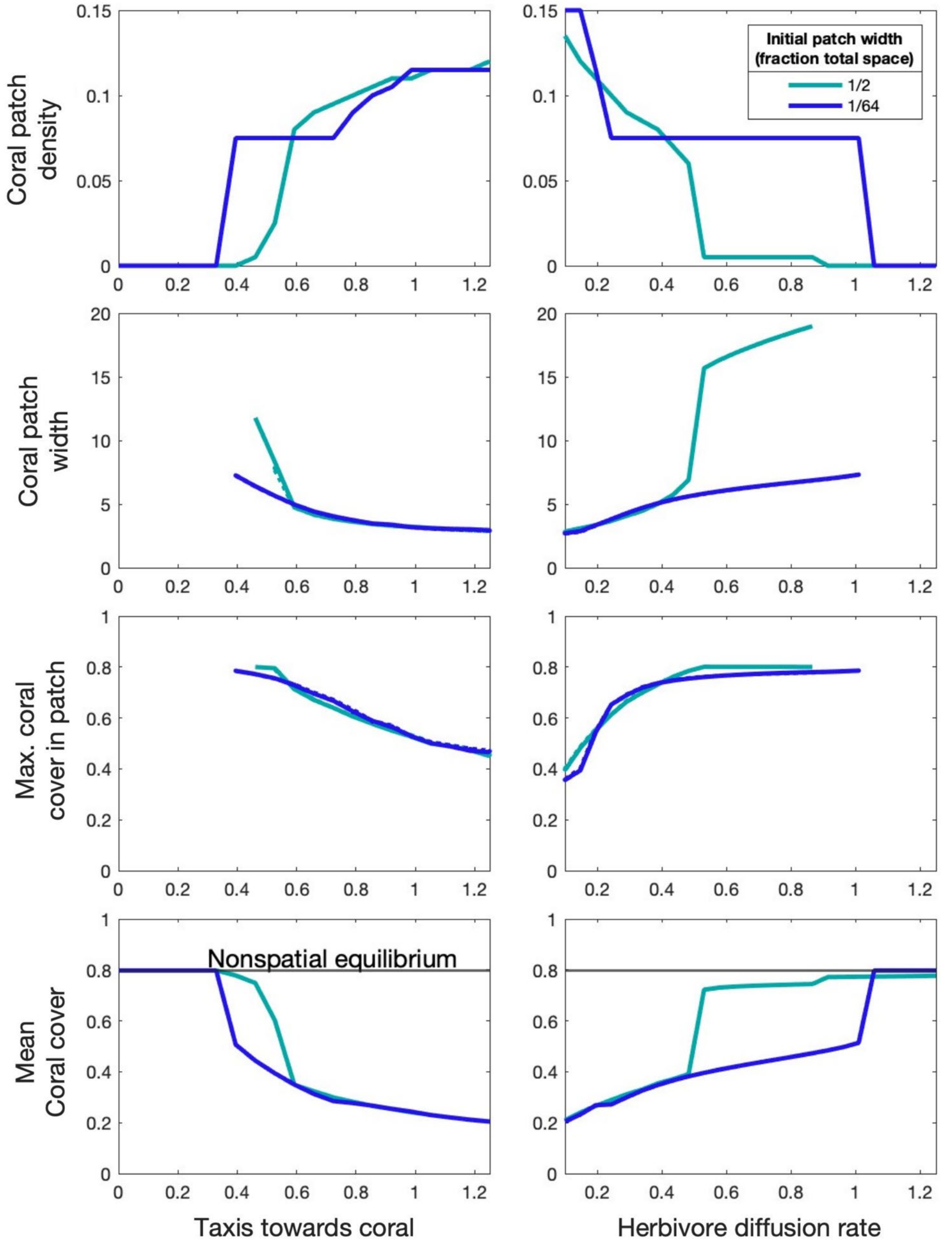

FIGURE 3 | Effect of strength of taxis towards coral (left column; the true values of τ_C are negative) and herbivore diffusion rate (right column) on coral patch characteristics for two sets of initial conditions. Fishing pressure was set to the same value used in the operating diagram in Figure 2 (0.1657 year^{-1}, just past the lower boundary of bistability). The first three rows show the density, width and height of the coral patches, respectively. For width and height, the values of the three patches closest to the center of the landscape are shown, but since the patterns were relatively uniform in all cases shown here, these lines are overlapping. The fourth row shows the spatially-averaged equilibrium coral cover, with the nonspatial equilibrium denoted with a horizontal line.

Our main findings were robust to the models describing local benthic dynamics (Figures S16–S19) and herbivore dynamics (Figures S12, S20–S22). Patterns did diminish when external herbivore recruitment approached their local growth rate r_H, but they only disappeared completely if the strength of taxis towards coral was sufficiently low (Figure S20).

In our model, herbivores with low diffusion that were strongly attracted to coral increased macroalgal dominance the most, as they drove the formation of patterns with the highest mean macroalgal cover and which persisted over the largest range of fishing pressures. When the system had two herbivore populations, with population A being 'pattern-forming' (low diffusion, strong taxis towards coral) and population B either ignoring or avoiding coral, population A could still cause pattern formation if it made up a sufficiently high proportion of the total herbivore community (Figure 4). However, the relative abundance of pattern-forming herbivores needed for a Busse balloon depended on the traits of the other herbivores in the community. For example, when population B avoided coral and had low diffusion, a higher proportional abundance of pattern-forming herbivores was needed to maintain patterns than when population B had no taxis at all (Figure 4).

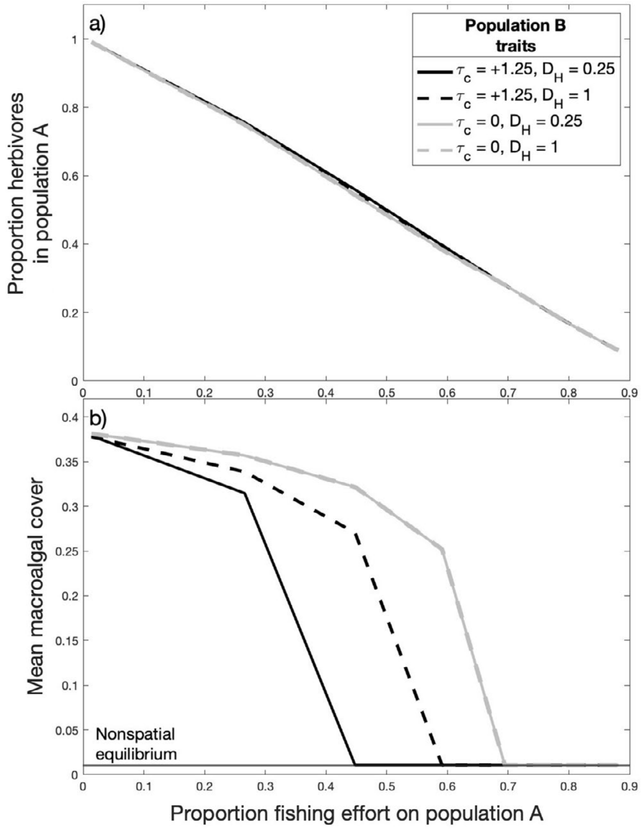

FIGURE 4 | Effect of fishing preferences on pattern formation in a system with two herbivore populations. Fishing pressures on each population were chosen such that total herbivore biomass remained at the value resulting from a fishing pressure of 0.1657 year^{-1} in the single herbivore model (just past the lower boundary of bistability). The *x*-axis shows the proportion of the total fishing pressure on population A, that is, $f_A/(f_A+f_B)$. In all cases population A is strongly attracted to coral and has a low diffusion rate ($\tau_C = -1.25\,\text{m}^2\,\text{C}^{-1}\,\text{year}^{-1}$, $D_H = 0.25\,\text{m}^2\text{year}^{-1}$). The traits for population B are indicated by line type and colour. (a) Proportion of the equilibrium total herbivore biomass made up of herbivores from population A. (b) Spatially-averaged equilibrium macroalgal cover, with the nonspatial equilibrium denoted with a horizontal line.

4 | Discussion

Preventing and reversing transitions between alternative stable states have emerged as pressing challenges in the Anthropocene, yet the ecological theory used to describe the dynamics of bistable systems remains largely nonspatial (Kéfi et al. 2022). Here, we used a suite of spatially explicit coral-macroalgal-turf models to show that herbivore behaviour (attraction to coral) can produce stable patterns that allow macroalgae to maintain local dominance at fishing pressures below the macroalgal-to-coral tipping point. The models thus predict the existence of a Busse balloon that increases the resilience of the macroalgal-dominated state, although the features of this balloon are highly dependent on herbivore movement traits and initial conditions. To our knowledge, this work provides the first example of a theoretical Busse balloon in coral reefs, opening many avenues for future research on how processes operating over continuous space mediate state transitions in these highly threatened ecosystems.

Effects of consumer behaviour on spatial patterning have been documented in numerous ecosystems, including boreal forests, grasslands, kelp forests and coral reefs (Adler et al. 2001; Pastor et al. 1998; Coppock et al. 1983; Smith et al. 2021; Madin et al. 2011). Consumers, particularly herbivores, can maintain existing spatial patterns and drive pattern formation (Adler et al. 2001). Theory predicts herbivore-induced pattern formation should be possible when grazing is spatially dependent (the surrounding landscape influences foraging decisions), positive feedbacks exist between grazing and site attractiveness (self-facilitation), and foraging is selective (De Knegt et al. 2008; Ge and Liu 2021). In our model, these conditions were met when herbivores were attracted to coral. In contrast, when herbivores avoided coral, there was no self-facilitation– and hence no patterns– because herbivores aggregated where macroalgal cover was high and grazed the macroalgae, enabling coral to become dominant and making these areas less attractive for themselves. Although herbivore avoidance of coral reduced or eliminated pattern formation in our model, this behaviour (and other mechanisms concentrating herbivores on macroalgae) can still promote coral resilience (Figure S3, Rassweiler et al. 2022). Theory also predicts patterns should only form when total herbivore abundance is at intermediate levels: if too low, herbivores will have minimal effects, and if too high, they can homogenise the landscape (De Knegt et al. 2008; Ge and Liu 2021; Weerman et al. 2011; Zhang et al. 2021). In our model, patterns only occurred at intermediate fishing pressures, emphasising that even when herbivores have traits that promote pattern formation, their overall abundance in the system ultimately drives benthic dynamics.

A key result from this study was the strong sensitivity of spatial patterning to herbivore movement traits. Formation of stable patterns required that herbivores were attracted to coral and that the strength of this attraction was sufficiently strong relative to their diffusion rate. These traits ensured most herbivores remained in or near coral patches, resulting in spatial variation in grazing pressure (intense grazing in coral patches and lower grazing in adjacent macroalgal patches) that reinforced patterns of alternating coral– and macroalgal-dominance. The strongest inhibitors of pattern formation were herbivores with low diffusion that avoided coral, and these herbivores could homogenise the landscape even when they made up only a small proportion of the herbivore community (Figure 4b). To begin exploring the extent to which herbivore communities on real reefs exhibit 'pattern-forming' or 'pattern-inhibiting' traits, we conducted a literature search on home ranges and substrate preferences of common herbivores in Moorea, French Polynesia (see Appendix S1 for details). Data on herbivore movement were sparse, and we therefore focused on broad categorizations rather than quantitative metrics (Table 2). Herbivores in Moorea appear to exhibit a range of movement traits, with some species potentially falling into pattern-forming (e.g., *Z. scopas*, *A. nigrofuscus*) and pattern-inhibiting (e.g., parrotfish) groups, and others having more intermediate trait combinations (e.g., *Naso* spp. may prefer coral but have relatively large home ranges). Based on the composition of the herbivore community (dominance of probable pattern-inhibiting species), our model would predict herbivore-driven pattern formation is unlikely in Moorea lagoons (although underlying spatial heterogeneity like bommie structure may support pattern formation through different mechanisms; Schmitt et al. 2019). However, the species most likely to be pattern inhibiting are also more heavily fished than species with pattern-forming traits (except for *Naso* spp.), suggesting variation in fishing pressure could have cascading effects on spatial dynamics. Future work should investigate whether spatiotemporal variation in the relative abundances of these species, as well as intraspecific variation in movement traits (see below), could lead to situations where herbivores generate and/or maintain heterogeneity in benthic cover on Moorea's reefs.

In addition to interspecific differences (Table 2), space use by individual herbivores is likely to be influenced by perceived predation risk and body size. Herbivores have been observed to shelter more in areas with high coral cover (Fong et al. 2018), and associations with coral/reef structure appear to be strongest for smaller individuals, especially those belonging to non-schooling species (Mumby and Wabnitz 2002; Gil et al. 2017; Johansson et al. 2012). Similarly, spatial scales of herbivore movement exhibit negative relationships with predator biomass but positive relationships with individual body size (Madin et al. 2010; Guerra et al. 2022; Nash et al. 2013). Thus, herbivores—particularly small, vulnerable individuals—may seek out and remain closer to areas with more coral/reef structure when perceived predation risk is high (one exception are juvenile parrotfish in Moorea, which associate with macroalgae like *Turbinaria*; Eggertsen et al. 2020). Predation risk is influenced by herbivore abundance: individuals use social cues to determine when it is safe to forage and are more willing to spend time out in the open when herbivore density is high (Gil and Hein 2017). Models predict this behaviour can lead to feedbacks that make the coral state more vulnerable to collapse when herbivores are fished, but enhance its ability to recover when fishing is reduced (Gil et al. 2020). However, if herbivores associate more strongly with coral (shelter) at low population densities, our model predicts full coral recovery might be hindered by the formation of persistent macroalgal patches. These effects could be exacerbated if fished populations have higher proportions of smaller individuals (Wilson et al. 2010), which may be less mobile and more attracted to coral than larger conspecifics. If the effects of fishing on herbivore space use are consistent across dominant herbivore species, fishing pressure may need to be reduced more than predicted by nonspatial models (and perhaps past the lower extent of Busse balloons predicted by spatial models lacking these behavioural feedbacks) in order to completely restore reefs to coral dominance.

Our model makes several simplifying assumptions that should be kept in mind when interpreting its predictions. To isolate the effects of herbivore space use, we ignored other aspects of herbivore functional diversity. Herbivores are generally grouped into guilds based on foraging traits, with each guild having distinct impacts on the benthic community (Green and Bellwood 2009). For example, grazers prevent macroalgal colonisation by removing new recruits, whereas browsers remove established macroalgae (Puk et al. 2020; Adam et al. 2022; Rasher et al. 2013). These contrasting roles, together with the range of movement traits within each guild (Table 2), may translate into more nuanced effects of herbivore communities on pattern formation. Beyond herbivory, there are other spatial feedbacks that could potentially lead to self-organised patterns not considered here, such as settlement feedbacks involving coral (e.g., coral larvae preferentially settling in areas with low macroalgal cover; Gleason 1996) and/or macroalgae (e.g., mature macroalgae providing a refuge for propagules settling nearby; Davis 2018). We also assumed environmental conditions were uniform across the landscape, as we were interested in whether patterns could form in the absence of underlying heterogeneity. On real reefs, however, key environmental parameters like fishing pressure, currents, nutrients and substrate suitability all vary across space (Holbrook et al. 2022; Rassweiler et al. 2022; Leichter et al. 2013; Lenihan et al. 2011), raising the potential for more complex patterns to arise from combinations of spatial feedbacks and underlying heterogeneity. For example, Byers and Noonburg (2007) demonstrated how fisher behaviour can interact with established marine reserves to influence the abundance of harvested populations that disperse between protected and unprotected areas, and such dynamics would likely have cascading effects on the herbivore-driven patterns in our model. Future work that relaxes our model assumptions should provide greater insight into the conditions under which Busse balloons occur in more realistic models of coral reefs.

Ecosystems are inherently spatial and may exhibit dramatic differences in community state over relatively small distances (Rietkerk and Koppel 2008; Smith et al. 2021). While theoretical work on alternative stable states has largely ignored space or treated it as discrete, a growing body of research is highlighting how models that allow for continuous spatial variation can reveal new insights into the dynamics of state transitions (Rietkerk et al. 2021). Our findings suggest that successful coral restoration may require 'popping' the Busse balloon (i.e., destabilising benthic patterns to allow for complete coral dominance, such as by focusing recovery efforts on herbivore populations that avoid coral). Coral reefs are just one of many ecosystems with alternative stable states, and analyses of spatially explicit

TABLE 2 | Feeding group classification, relative abundance, movement traits and fishing status (from Rassweiler et al. 2020) of the most common herbivores in each feeding group in Moorea, French Polynesia. See Appendix S1 for more details.

Species	Feeding group	% Total herbivore biomass	Home range	Taxis	Fished	Refs
Scarus psittacus	Scraper	17.67	Medium	Turf (likely)	Yes	Howard et al. 2013, Chow et al. 2021, Han et al. 2016
Chlorurus spilurus	Excavator	17.51	Medium	Turf (likely)	Yes	Davis et al. 2017; Eggertsen et al. 2020, Chow et al. 2021, Han et al. 2016, Tootell and Steele 2016
Ctenochaetus striatus	Detritivore	25.35	Small	Macroalgae	No	Chow et al. 2021, Munsterman et al. 2021
Acanthurus nigrofuscus	Grazer	4.18	Small	Turf/macroalgae (foraging), coral/bommie/reef structure (shelter)	No	Tootell and Steele 2016, Fischelson et al. 1987, Gil et al. 2017, Santano et al. 2021
Zebrasoma scopas	Grazer	5.71	Small	Coral (juvenile); no preference/preference for turf (adult), reef structure	No	Robertson et al. 1979, Chow et al. 2021, Claisse et al. 2009, Gil et al. 2017
Siganus spinus	Browser (but not *Turbinaria*)	0.87	Large (likely)	Coral, or at least macroalgal avoidance	Yes	Fox and Bellwood 2011, Chow et al. 2021, Cheal et al. 2010, Gil et al. 2017
Naso lituratus	Browser	0.24	Medium/large	Coral	Yes	Marshell et al. 2011, Ford et al. 2016
Naso unicornis	Browser	0.20	Medium/large	Coral	Yes	Meyer and Holland 2005, Chow et al. 2021, Marshell et al. 2011, Ford et al. 2016

models like the one we present here should improve our understanding of how spatial feedbacks influence the dynamics of these systems.

Author Contributions

All authors discussed concepts and ideas. A.R.D. and H.V.M. built the models; A.R.D. and S.D.M. constructed the herbivore traits table; and A.R.D. ran all model analyses, created the figures and drafted the manuscript. All authors reviewed and edited manuscript drafts.

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Data Availability Statement

The data and code supporting the findings of this study are openly available in Zenodo (https://doi.org/10.5281/zenodo.13730757) and from the EDI Data Portal (https://doi.org/10.6073/pasta/a7430f5a775040873df9b8571fd9d3cd).

Peer Review

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Endnotes

[1] With respect to the spelling of Moorea, we followed the *Raapoto* transcription system that is adhered to by a large segment of the Tahitian community, but also recognise other community members follow the Te Fare Vanā'a transcription system where the island name is spelled with an 'eta' (Mo'orea) (see mcr.lternet.edu/spelling_of_Tahitian_place_names).

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.