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Monitoring the fabric of nature: using allometric trophic network models and observations to assess policy effects on biodiversity

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Species diversity underpins all ecosystem services that support life. Despite this recognition and the great advances in detecting biodiversity, exactly how many and which species co-occur and interact, directly or indirectly in any ecosystem is unknown. Biodiversity accounts are incomplete; taxonomically, size, habitat, mobility or rarity biased. In the ocean, the provisioning of fish, invertebrates and algae is a fundamental ecosystem service. This extracted biomass depends on a myriad of microscopic and macroscopic organisms that make up the fabric of nature and which are affected by management actions. Monitoring them all and attributing changes to management policies is daunting. Here we propose that dynamic quantitative models of species interactions can be used to link management policy and compliance with complex ecological networks. This allows managers to qualitatively identify 'interaction-indicator' species, which are highly impacted by management policies through propagation of complex ecological interactions. We ground the approach in intertidal kelp harvesting in Chile and fishers' compliance with policies. Results allow us to identify sets of species that respond to management policy and/or compliance, but which are often not included in standardized monitoring. The proposed approach aids in the design of biodiversity programmes that attempt to connect management with biodiversity change.

This article is part of the theme issue 'Detecting and attributing the causes of biodiversity change: needs, gaps and solutions'.

1. Introduction

It is now abundantly clear that the diversity of species supports the essential ecosystem functions for life on the planet, including ours [1]. The relationship is not simple, nor homogeneous across terrestrial and marine ecosystems, but empirical data show that the richness of life is critical for function and persistence [2–4]. In the oceans, one of the most tangible ecosystem services provided by biodiversity is the production of nearly 200 million tons of fish, invertebrate and macroalgal biomass that is extracted yearly from wild or cultured populations at sea [5]. This biomass is essential for human food security and health [5], and its importance

will increase in the future [6]. The vast amounts of fished marine biomass result from a myriad of marine organisms, many of them seemingly insignificant, which determine the growth, reproduction and survival of exploited species, i.e. the fabric of nature [7]. The roles of different species vary widely, from keystone to redundant or apparently insignificant. Their attributes vary as well, from rare to hugely abundant, from tiny to enormous, from sessile to highly mobile, from conspicuous to cryptic. Cataloging the species richness that sustains ecosystem services, and attributing changes to management policies, is therefore daunting. Many have highlighted the challenges of regional, national and international biodiversity monitoring programmes and have proposed a wide variety of principles, rationale and approaches, which attempt to strike a balance between what is needed and what is feasible for nations and regulatory agencies [8–13]. Adaptive monitoring is one of the foundations of Ecosystem Based Management (EBM) programmes and several principles have been laid down to connect biodiversity and management [14–16]. Here we are concerned with regional-scale monitoring programmes that aim at identifying and attributing causes of biodiversity changes to specific policies and human activities in managed ecosystems. We focus on the community-wide impacts of harvesting the kelp *Lessonia spicata* on the coast of Chile to illustrate how an Allometric Trophic Network (ATN) model can be used to identify species to be included in diversity monitoring programmes and link management policies to biodiversity change.

We submit it is nearly impossible to monitor all biodiversity of any real ecosystem, at least not in the complete manner that we require to assess the impact of our actions and our management practices on the fabric of nature. Huge advances have been made in systematically documenting diversity over large, sometimes global spatial and long time scales [17–19]. The past decades have seen great achievements in molecular techniques to decipher diversity (e.g. the use of e-DNA [20,21]), and new methodologies to detect, quantify and explore uncharted habitats, especially in the oceans. But despite these advances and improved global diversity compilations [18,22] and statistical techniques to estimate richness [23], we have to humbly recognize we do not know precisely how many and which species co-inhabit in any given ecosystem on Earth. Our most complete databases are taxonomically constrained assemblages (e.g. breeding birds, reef fish, Barro Colorado Island angiosperms), artificially delimited habitats (e.g. ‘coastal marine rocky shores’), size-truncated communities (macroscopic molluscs), etc. We know that a realistic measure of biodiversity that links to ecosystem processes cannot consider birds and exclude the insects on which birds feed. We know that coastal marine invertebrates are eaten by rock fish and birds, and their larval stages live and interact in the plankton with thousands of plankters. We know that pollinators of angiosperm plants are critical for plant persistence and any account of local forest diversity useful to understand dynamical processes, must include their pollinators as well as the soil diversity on which plants depend. We know that our most complete catalogues of biodiversity today have left out parasites and the hundreds to thousands of microbial organisms with which we coexist. These are not disconnected ‘microbial loops’ or ‘microbiomes’; they also are critical components of the fabric of nature [24,25].

From the gloomy but realistic account above it should be obvious that there is no silver bullet approach that can assess

human impacts on all components of biodiversity [14,26]. Single, ‘one for all’ standardized protocols will not do. Solely cataloguing species in space and time will not be sufficient to assess impacts on biodiversity and connect those impacts to policy. Given the virtual impossibility of monitoring all species, we need to anticipate which ones will most likely change, and design specific monitoring programmes for those species across regional scales. This requires an understanding of species interactions. We illustrate how models of species interactions of intermediate to high complexity, which have been delineated before by many [16] and recently used to study species range shifts [27], can be coupled with management policies to generate scenarios that allow us to identify which species will most respond to specific policies.

2. Biodiversity monitoring programmes: the need for interaction-based approaches

The body mass (W) abundance (D) relationship, one of the most universal relationships characterizing assemblages and communities in nature [28–30], serves to illustrate the common strategies used to monitor biodiversity, as well as their limitations. It is a particularly nice template to examine diversity changes since anthropic activities are also known to alter body size spectra [18,31]. Not all species in the D – W spectrum are equally considered in standardized monitoring programmes within a region. On one extreme, large-bodied, typically less abundant species are targeted for monitoring programmes in conservation and management (figure 1, region A). Several ‘emblematic’ and ‘sentinel’ species of EBM plans fall in this category (e.g. sea otters, whales, marine iguanas, many birds). Dominant plant species and mammals are also common targets of monitoring. It can be argued that these species are ‘indicators’ or ‘sentinels’ of the state of biodiversity or ‘health’ of the ecosystem. A similar argument can be made about monitoring ‘keystone’ species, as defined by their disproportionate impacts on community attributes [32] and several conservation programmes have followed these principles to focalize their resources [33]. Focusing biodiversity monitoring on keystone species has allowed us to maximize the use of resources allocated to protected areas, and also guided the reintroduction and recovery of keystone predators that had been extirpated from communities (e.g. wolves in Yellowstone National Park). Attributing changes in these target species to specific policies is generally feasible. On the other extreme (figure 1, region B), the onset of high-quality remote imagery to monitor biodiversity has in many ways changed the game for ecologists, oceanographers, geographers and climate change scientists. The capacity to observe, over large spatial scales, indicators of multi-species plant cover, phytoplankton biomass, etc. makes it possible to inexpensively measure many integrated biodiversity variables [17]. But these integrated measures are usually dominated by few species, of a wide range of body sizes (phytoplankton, trees), and can obscure changes occurring in many less abundant or rare species within the assemblage or guild (e.g. less abundant phytoplankton, understory trees). Exceptional monitoring programmes for small organisms, such as vessel-based microbial recording [34], can change our understanding of biodiversity in the ocean, but attribution of change to policy will remain a major challenge.

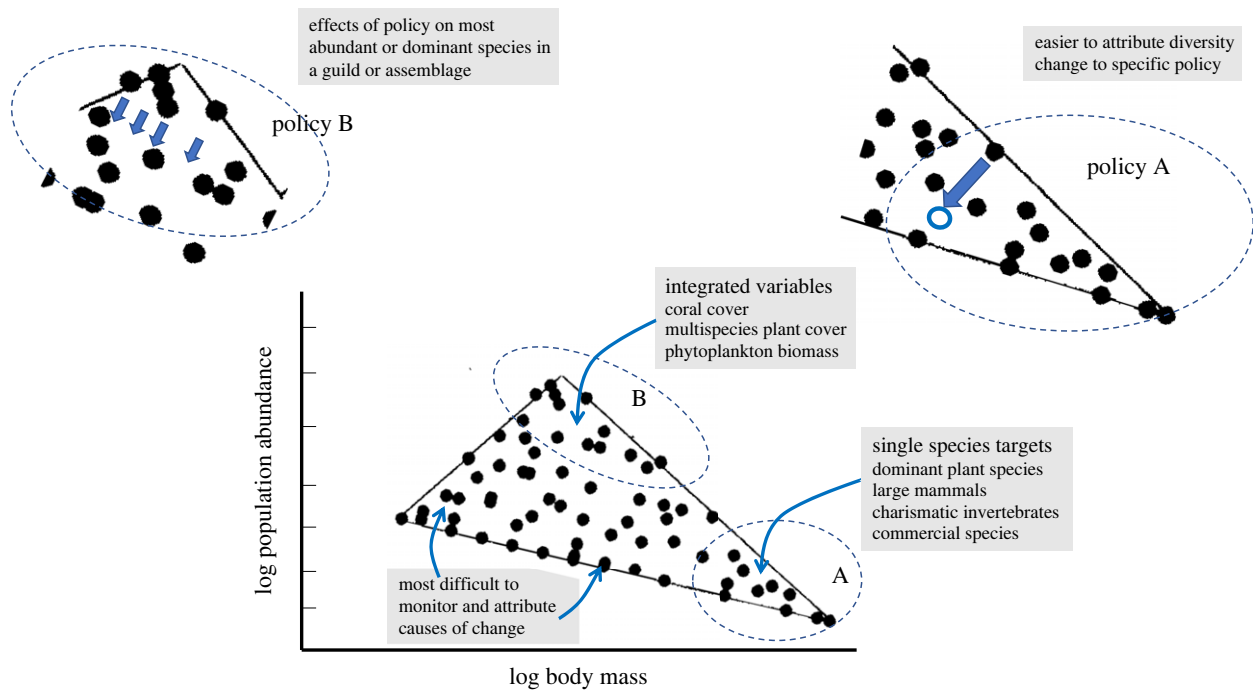


Figure 1. The scaling of population abundance and body mass that characterizes most assemblages and communities within a given region or ecosystem in log-log scale. The very large species in the bottom right are typically included in designed or ‘target’ monitoring programmes of biodiversity. Attributing changes in abundance of these species to specific policies is comparatively easy. The very abundant species at the top of the abundance-body mass plane usually account for a large fraction of the integrated variables of abundance that form part of monitoring programmes (e.g. multispecies plant cover, phytoplankton biomass). Changes in these integrated variables, as a consequence of human activities, reflect well the changes in the dominant species, but not necessarily the magnitude or direction of change in the less abundant species within the assemblage.

Changes in ‘indicator’ species or in integrated variables are useful for many purposes, but they may not be the best targets to connect fishery policies with biodiversity changes. Propagation of fishery alterations through the ecological web cannot be assumed to be linear, proportional or even in the same direction to the magnitude of the alteration. The problem of propagation of species interactions was brightly captured in Yodzis’s ‘indeterminacy of ecological interactions’ over 30 years ago [35]. Basically, alteration of one species biomass will have positive, negative or negligible effects on abundance and persistence of other species that are not directly connected to the target one, potentially driving them to extinction or to a pest status (e.g. release from top-down control). The affected species may fall in the D–W spectrum hardest to include in standardized monitoring programmes, but yet they may be strongly correlated with ecosystem functions [1].

3. Beyond species lists: guiding the consequences of management strategies

One of the main goals of biodiversity monitoring programmes is to infer the causes of ecosystem change, being they global or regional in scope [15]. As Yoccoz stated, ‘this is required for management, when different actions are possible and their consequences need to be assessed and compared’ [14]. Indeed, adaptive monitoring is one of the foundations of EBM [11,36]. But attributing the causes of change from spatio-temporal patterns of biodiversity is difficult. Yodzis illustrated the virtual impossibility of making sound management decisions for Benguela fisheries without knowledge of species interactions in the community. Like fisheries biologists

before him [37], Yodzis advocated the use of multi-species models of intermediate or high complexity to guide ecologically sustainable management decisions. Dependency on the values of many parameters, for which reasonable estimates or good biological guesses must be made, is typically the major limitation of the approach when it comes to recommending a fishing quota, defining biological reference points, or providing the basis for EBM planning. Here we submit that multi-species dynamic and quantitative models can be used to qualitatively assess which species in an ecosystem are affected by management decisions and levels of compliance with policies. While management decisions are highly dependent on parameter values, we argue that, in most ecosystems, identifying the species that are indirectly affected by a given management plan is relatively insensitive to the chosen parameters, partly because the topological structure of the ecological network establishes the main paths of interaction propagation. Thus, realistic models of species interactions can be used to produce scenarios that allow us to link management policies with ‘interaction-indicator’ species. If biodiversity assessments show that these ‘interaction-indicator’ species are changing as anticipated by models, attributing causes of diversity change seems possible.

4. Which species are most affected by different management policies? The case of harvesting Chilean intertidal kelps

Management strategies and policies have to balance the putative effect of the policy on the target species, and the level of compliance. Non-compliance can undermine management

Table 1. Recommendations for harvesting kelps *Lessonia* spp. incorporated in the fishery regulations, which are largely based on Vásquez [48]. Expected effects of compliance and non-compliance to these recommendations on the *Lessonia* kelp forests are presented and we indicate how they were represented in the model.

harvesting recommendation	compliance fishing scenario	non-compliance fishing scenario
1. harvest less than 25% of the standing stock	fishers leave about 75% of the adult plant biomass modelling: $F_{\max} \leq 0.009$ (to remove ca. 20% adult biomass)	fishers remove in excess of 25% of the standing stock not modelled
2. remove only adult plants	fishers harvest only adults modelling: F_{\max} applied only to adult stages	fishers harvest adults and juveniles not modelled
3. remove entire holdfast to facilitate recruitment	fishers remove entire plants modelling: no delay (time lag) between application of fishing mortality and effect on juvenile plants and competition	full compliance
4. remove one out of every three plants to facilitate recruitment	fishers leave sparse adults in the field modelling: the intrinsic growth rate of new plants (recruits) is set at $r_j = 0.02857$ with $F_{\max} \leq 0.009$	fishers leave large barren areas modelling: the intrinsic growth rate of new plants (recruits) is set at $r_j = 0.02857 * \text{factor}$, with $\text{factor} = 0.001$ and $F_{\max} \leq 0.009$

regimes and create tensions between resource users and regulators, ultimately affecting the sustainability of stocks and marine ecosystems [38,39]. Social, institutional, behavioural and economic motivations affect compliance [40–42]. Studies which address non-compliance have generally focused on exploring the underlying motivations for people to comply with regulations [43], or on the opportunities the immediate environment generates for non-compliance. Accordingly, understanding compliance is complex and should include both context-specific drivers and an assessment of underlying human motivations. In any case, non-compliance in coastal fisheries is one of the main threats to spatial co-management policies [44,45]. Here we focus on the biodiversity effects of non-compliance.

On the wave-exposed rocky shore of central Chile there is abundant information about species richness and ecological interactions [46,47]. We used harvesting of the intertidal kelp ‘huir negro’, *Lessonia spicata*, as a model to assess which species could be most sensitive to fishing scenarios and compliance to regulations. Intertidal and subtidal kelps are extracted by coastal fishers and used as raw and dried commodities [48], representing between 50% and 70% of the total seaweed landings [49] and from this, *L. spicata* accounts for more than half. Foreign markets impelled *Lessonia* fisheries since the mid 2000s and increased unregulated extraction of these habitat-forming species, especially in northern Chile [50]. Regulations were recently implemented based on basic aspects of growth and reproductive biology of these species (table 1). High levels of illegal harvesting (non-compliance) exist [51], which can have large impacts on the sustainability of the fisheries.

Lessonia spicata is a competitively dominant species that forms a characteristic band in the low intertidal zone of wave-exposed habitats [46,52]. Adult plants have large holdfasts (around 40 cm diameter), stiff stipes that can reach about 60–80 cm vertically above the rock at low tide, with fronds up to 2 m long. Canopy cover can reach 90–100%, but holdfasts are typically spaced apart [53]. Large grazers are uncommon in the understory, apparently because of the mechanical action (whiplash) by fronds and stipes [53,54].

Several grazer species can feed on *Lessonia* juveniles, but very few feed on adult plants [54]. One of them is the scurrinid limpet *Scurria scurra*, which lives on the stipes and creates a ‘home’ cavity while feeding on the outer layers of the stipe and on epiphytes [55,56]. While gametophytes recruit more intensively among adults, juvenile plants are notoriously absent from the understory and grow best in small clearings, at some distance (few metres) from the adults, but they are completely unsuccessful in larger clearings [53,54] (figure 2). Plants do not regenerate from the holdfasts. Harvesting regulation thus dictates that plants must be removed whole, harvesting should be less than about 25% of the standing stock, only adult plants (holdfasts greater than 20 cm diameter) should be harvested, and only about one in every three plants should be removed to facilitate kelp recovery (table 1, figure 2).

The model described in detail below attempts to capture the essential elements of the system as depicted in figure 2, and simulates scenarios that reproduce harvesting under proposed regulations, and non-compliance with one of them: removing one every three adult plants (figure 2b). We first evaluate the propagation of the effects of harvesting *Lessonia* with respect to an unfished ecosystem. The system transformations that occur following ‘legal’ fisheries is used as our reference state to model whether non-compliance can have additional effects on other species, which should then be the targets for monitoring. Since fishers sell plants by total weight, non-compliance with regulation 3 (table 1, removing entire plants) is rare. We therefore focus on the effects of fishing recommendation 4 (table 1, removing one every three plants).

Our approach here is conservative as far as assessing the impact of *Lessonia* harvesting on other species. Our goal is to illustrate how these types of global models can be used to raise awareness about the effects of regulations and focus monitoring programmes on otherwise ‘unsuspected’ species. The macroalgal components in this model system are very sensitive to fishing mortality and it has been shown that over-exploitation can cause extinctions of other species [57]. Secondly, and more importantly, *L. spicata* is one of the most important habitat-provider species in the intertidal community, establishing a large number of negative and

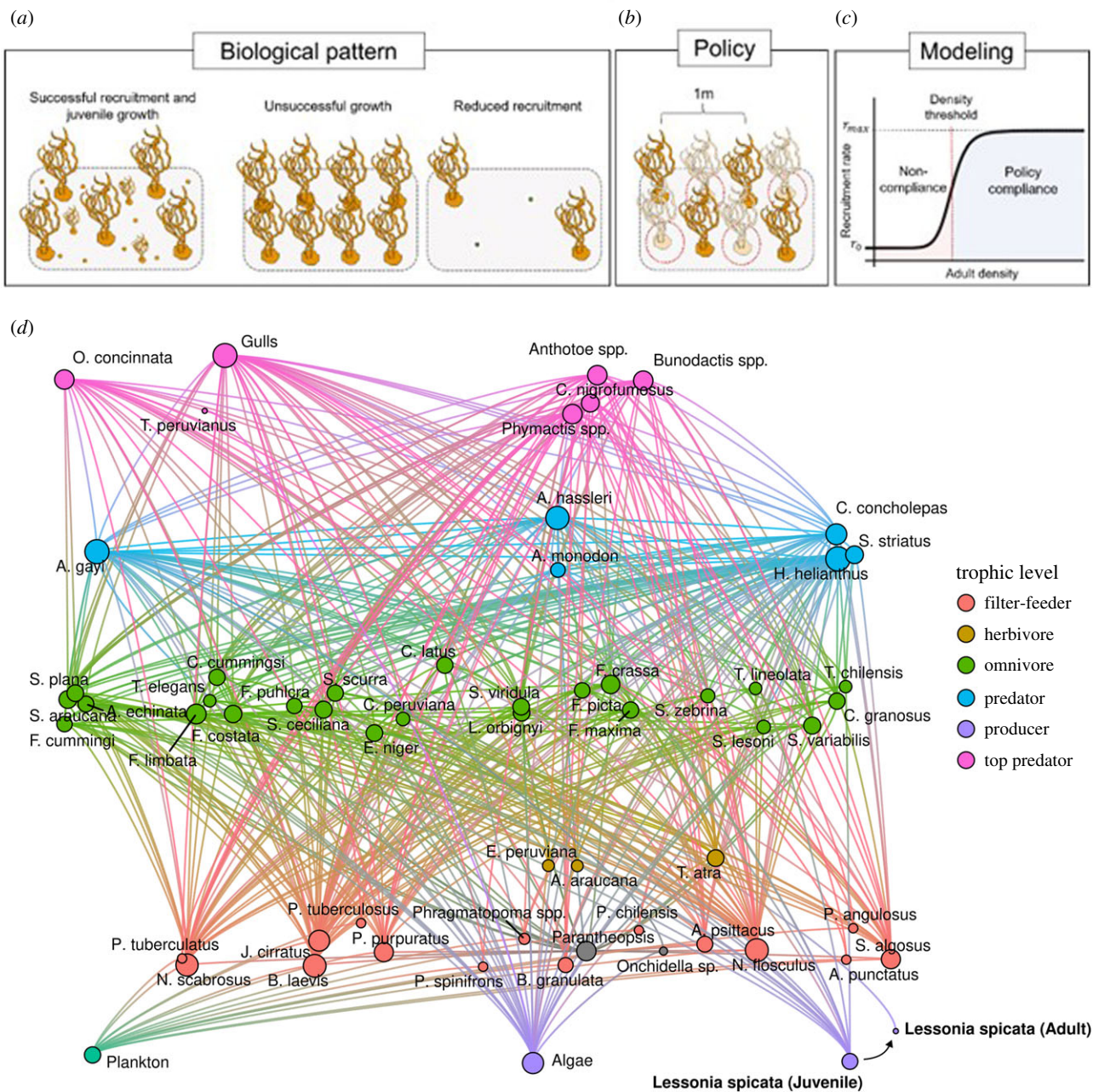


Figure 2. (a) Graphical representation of the main biological pattern in the recruitment and growth of *Lessonia*, in which both processes are maximal when the densities of *Lessonia* are intermediate. (b) Management recommendations (table 1) follow this biological effect, by targeting an intermediate density of plants to maximize recruitment, and thus production. (c) Non-compliance with those recommendations can result in a reduced recruitment rate in *L. spicata* forests below a given density threshold, which was included in our model. (d) The ecological network in which *L. spicata* is embedded. For the sake of simplicity of the example shown here, we pooled macroalgal species (except *Lessonia*) into one node (Algae).

positive non-trophic interactions with other species in the community [47]. We have left these non-trophic interactions out of the example shown here, except for interference competition with other algae and sessile filter feeders. The behaviour of the food web component of this ecological network has been better studied [57] and its parameterization follows standard bioenergetic approaches.

5. Methods

(a) Model description

The simulations are based on a widely used, allometry-based bioenergetic (Allometric Trophic Network, ATN) model, which is primarily based on Yodzis & Innes' [58] equations for consumer interactions and facilitates parameterization, while gaining

some level of mechanistic understanding of the entire community of interacting species [59]. In our case, we modelled the intertidal species co-occurring in wave-exposed rocky platforms of central Chile [47,60]. To reproduce the basic ecological aspects of *L. spicata* and the management scenarios in table 1, we use a two-stage population model that includes inter-dependent juvenile and adult plants. For the sake of simplicity and because of scarce species-specific growth data, other macroalgal species (figure 2c, algae) were pooled into a single macroalgal node, retaining the outgoing links (consumers) of the group. We therefore can focus on changes occurring in invertebrate species only. The model thus reduced the original 106 species to a total of 60 taxonomic species and 60 + 1 (juvenile *Lessonia*) nodes. Thus, the nodes at the base of the food web include three different types of primary producers: (i) all macroalgae (ii) juvenile *Lessonia*, (iii) adult *Lessonia* and (iv) filter-feeders, which are not autotrophic, but use plankton originating from outside the modelled system.

Non-*Lessonia* macroalgae grow logistically and are being consumed by herbivores, and thus have temporal dynamics given by the following equation:

$$\frac{dB_i}{dt} = \underbrace{r_i B_i \left(1 - \frac{B_i + B_J + B_A + B_F}{K}\right)}_{\text{logistic growth}} - \underbrace{\sum_{j \in \text{herbivores}} x_j y_{ji} B_j F_{ji}(\mathbf{B})}_{\text{herbivory}} \quad (5.1)$$

where B_i represents the biomass of the focal species (here non-*Lessonia* algae), B_J and B_A the biomasses of juvenile and adult *Lessonia*, respectively, and B_F the total biomass of sessile filter feeders (e.g. mussels). r_i is the intrinsic growth rate of algae (which is included as an average for all algae in this model example), and K the total carrying capacity of the system, which considers space as a limited resource. Therefore, algae can compete with sessile animal species. The herbivory term represents a standard consumption term for this type of model, in which x_j is the metabolic rate of consumer j , y_{ji} is the attack rate of consumer j on prey i , and B_j is the biomass of consumer

j . $F_{ji}(\mathbf{B})$ represents the multi-species functional response, which describes the rate at which species j consumes species i given the biomasses \mathbf{B} of all species in the system and takes the form:

$$F_{ij}(\mathbf{B}) = \frac{\omega_{ij} B_j^q}{B_{0,ij}^q + d_i B_i B_{0,ij}^q + \sum_{l \in \text{resources}} \omega_{il} B_l^q}$$

where ω_{ij} is the preference of species j for species i , $B_{0,ij}$ is the consumer biomass at which F_{ij} is half of its maximum and d_i is the intensity of predator interference for species i , i.e. how much that species reduces the ability of others to consume prey. q is an exponent which determines the type of functional response, with $q=1$ being a type-II functional response and $q=2$ a type-III functional response [29].

The dynamics of juvenile *Lessonia* biomass (B_J) are determined by logistic growth, consumption by herbivores and omnivores, natural mortality and harvesting ($F_{\max,J}$). Juveniles are also lost from the population because they grow into adults:

$$\frac{dB_J}{dt} = \underbrace{r_J B_A \left(1 - \frac{B_J + B_A}{K_A}\right)}_{\text{reproduction}} - \underbrace{\sum_{j \in \text{herbivores}} x_j y_{ji} B_j F_{ji}(\mathbf{B})}_{\text{herbivory}} - \underbrace{P_{J \rightarrow A} \left(1 - \frac{B_A}{K_A}\right) B_J}_{\text{change into adult stage}} - \underbrace{F_{\max,J} B_J}_{\text{extraction}} \quad (5.2)$$

$F_{\max,J}$ is the fraction of juvenile *Lessonia* biomass harvested commercially. In all the simulations $F_{\max,J}=0$, i.e. full compliance with regulation 2 in table 1. For simplicity we assume that juveniles are all the same size (they do not grow) and therefore, the increase in juvenile biomass is due only to new individuals at a rate controlled by a per biomass adult reproductive rate, r_J , multiplied by reproductive adult *Lessonia* biomass, B_A . We considered that if no adult plants are left in the system, no juveniles are produced (there is no subsidy of gametophytes from external sources). Field observations suggest that *Lessonia* is not significantly affected by competition with other sessile species and therefore, maximum production rates is only limited by total *Lessonia* biomass. The passage of juvenile *Lessonia* into the adult stage is controlled by a rate parameter $P_{J \rightarrow A}$, which is set based on the fact that plants reach 20 cm holdfast diameter in about one year. The transformation of juveniles into adult plants is strongly limited by the presence of adults, B_A , in the system through the term $(1-B_A)/K_A$, with K_A thus representing a carrying capacity for adult *Lessonia* plants. At carrying capacity, K_A , new juveniles are produced (gametophytes), but cannot successfully grow because of shading, whiplash by adult plants, lack of space and/or nutrients. It is important to note that K_A is different from the overall carrying capacity of the system K . We used a different K_A , because (i) *Lessonia* are dominant competitors and are little affected by competition for space with other species, and (ii) the mechanisms of interference for space among *Lessonia* plants are qualitatively different than those of other algae. Kelp compete for space with each other, not by covering all the available substratum, but by interfering with each other at the canopy level, much like dominant trees in a forest. Thus different parameters and mechanisms for growth limitation reflect the ecological mechanisms better (figure 2).

The dynamics of adult *Lessonia* are given by the addition of juveniles into the adult stage, minus the losses due to herbivory and extraction:

$$\frac{dB_A}{dt} = \underbrace{P_{J \rightarrow A} \left(1 - \frac{B_A}{K_A}\right) B_J}_{\text{change into adults}} - \underbrace{\sum_{j \in \text{herbivores}} x_j y_{ji} B_j F_{ji}(\mathbf{B})}_{\text{herbivory}} - \underbrace{F_{\max,A} B_A}_{\text{extraction}} \quad (5.3)$$

The fraction of adult biomass extracted commercially per unit of time is given by $F_{\max,A}$, the fishing mortality. All other terms as before.

We separated the dynamics of heterotrophic consumers (both primary and secondary) into filter feeders and other consumers. Filter feeders are usually considered basal species because they feed on an external source to the benthic community, 'plankton', which is controlled primarily by advective-hydrographic processes. From the point of view of the focal community, the plankton represent a subsidy to filter feeders. So, the filter feeder dynamics can be represented as:

$$\frac{dB_F}{dt} = \underbrace{f_F x_F s B_F \left(1 - \frac{B_F + B_A + B_J + B_i}{K}\right)}_{\text{consumption}} - \underbrace{\sum_{j \in \text{predators}} x_j y_{ji} B_j F_{ji}(\mathbf{B})}_{\text{predation}} - \underbrace{f_m x_F B_F}_{\text{maintenance}} \quad (5.4)$$

Here f_F represents the efficiency of plankton consumption, x_F the metabolic rate of filter feeders, s is the external subsidy of plankton, which in our simulations is always positive and non-limiting, so that in the absence of consumption, filter feeders grow to allowable carrying capacity in the system, K , which captures competition with other sessile species. For non-sessile filter feeders (e.g. porcelain crabs) we did not consider competition with other sessile species. f_m represents the fraction of the consumer biomass lost by respiration for the maintenance of basal metabolism.

The dynamics of non filter-feeder consumers (herbivores, omnivores, carnivores) followed the traditional drivers in bioenergetic models, including gains thanks to prey consumption, and losses due to predation and natural mortality scaled to respective size-based metabolic rates:

$$\frac{dB_i}{dt} = \underbrace{f_i x_i B_i \sum_{j \in \text{resources}} y_{ij} F_{ij}(\mathbf{B})}_{\text{consumption}} - \underbrace{\sum_{j \in \text{predators}} x_j y_{ji} B_j F_{ji}(\mathbf{B})}_{\text{predation}} - \underbrace{f_m x_i B_i}_{\text{intrinsic mortality}} \quad (5.5)$$

(b) Parameterization

The parametrization follows the approach described in Ávila-Thieme *et al.* [57], which builds upon a widely used approach based on allometric relationships to provide realistic model coefficients [58,61,62], along with modifications for aquatic systems [63]. The biological rates of production R , metabolism X and maximum consumption Y , follow the empirically observed power-law relationships with a $-1/4$ exponent [59,64]:

$$R = a_r M_P^{-0.25}$$

$$X = a_x M_C^{-0.25}$$

$$\text{and } Y = a_y M_C^{-0.25}$$

where a_r , a_x and a_y are constants, and M_P and M_C are the body masses of producers and consumers, respectively.

The time scale used to determine the dynamics of the system is defined based on the producer with the highest mass-specific growth rate R (here, plankton). We normalized the production rate, metabolism and consumption by those of the reference species, yielding the following equations for r_i , x_i and y_i for each species i :

$$r_i = \frac{R_P}{R_{P,\text{ref}}} = \left(\frac{M_P}{M_{P,\text{ref}}} \right)^{-0.25},$$

$$x_i = \frac{X_C}{R_{P,\text{ref}}} = \frac{a_x}{a_r} \left(\frac{M_C}{M_{P,\text{ref}}} \right)^{-0.25}$$

$$\text{and } y_i = \frac{Y_C}{X_C} = \frac{a_y}{a_x}.$$

Parameter values followed those in the model described in Ávila-Thieme *et al.* [57], which include the same species of our model (electronic supplementary material, table S1). Since we aggregated all non-*Lessonia* algae in one node, we recalculated the species biological production rates (electronic supplementary material, table S1). As we discuss below, the per biomass algal production rates are scarcely known for marine intertidal systems.

We simulated single-species management by changing F_{max} for adult *Lessonia* and examined the effects on other species' biomass. Under the unfished scenario, $F_{\text{max}}=0$ for juvenile and adult *Lessonia*. The compliance to harvesting regulations corresponds to $F_{\text{max},A}=0.009$ (leading to 20% of adult standing biomass removed), $F_{\text{max},J}=0$, thus assuming fishers do not remove juvenile plants (compliance with regulation 2, table 1). We assume that in this compliance case effective plant fecundity (juvenile growth rate) was maximum, with $r_j=0.02857$ (table 1). The non-compliance scenario modelled here was the removal of adults within the total biomass fishing limit of <25% ($F_{\text{max},A}=0.009$), but not keeping the maximum distance of 1 m between adults, which, according to literature, severely reduces new plant growth. This means fishers keep the recommended standing biomass of adult plants over a large area, but clear large spaces within. We used an arbitrary factor of 0.001 reduction in *Lessonia* juvenile growth (table 1) to simulate a severe growth limitation in the absence of nearby adult plants. Scarce information exists to provide a more continuous and mechanistic assessment of this effect. Intertidal experiments showed that clearing adult *Lessonia* plants allowed grazers to come in and prevented juvenile growth [53,54], and 'barren grounds persisted for several years' [54]. Subtidal experiments with another *Lessonia* species, *L. trabeculata*, showed similar effects of creating large spaces among adult plants [54], with experimental clearings lasting at least over the 2 years of the experiment [65]. Thus, available information suggests severe limitation of juvenile plants, but there is not enough information to model this as a function of distance or size of the barren area. In all cases, simulations involved setting the initial species biomasses to their empirical, average biomasses observed through 6 years of

sampling in central Chile (see [57], for details) and running the model 15 000 time steps, until a steady state was reached. Resulting species abundances were considered the 'unfished' condition of the system. We then applied the *Lessonia* extraction according to the compliance and non-compliance scenarios described above, and let the system run until a second equilibrium was reached. We compared the biomasses of species at equilibrium before and after the application of fishing mortality. The dynamical model was simulated using ODE15s in Matlab.

(c) Sensitivity analysis

To provide recommendations regarding the species to include in diversity monitoring programmes, a sensitivity to parameter values must be conducted. Results are used to identify which additional species in the ecological web may also change more than some reference value (e.g. 5%), when we use different parameter values. Precautionary principle dictates that if additional species change in abundance, they should be candidates to monitoring programmes. We did not carry out a full sensitivity analysis of parameters in the ATN model as previous studies have focus on their ability to reproduce observed patterns and robustness [59,63]. We focused on four parameters specific to our system: (1) *Lessonia* fishing mortality, $F_{\text{max},A}$. We used scenarios for $F_{\text{max},A}$ between 0.001 and 0.01, which allowed maintaining compliance with fishing regulation (removing <25% standing biomass). Using higher fishing mortalities should be part of a more complete sensitivity analysis, but it corresponds to a different non-compliance scenario. (2) The rate at which juveniles become adults, $P_{J \rightarrow A}$. We used 1001 values between 0 and 1 at 1/1000 increments. The same values were applied to unfished and fishing compliance scenarios. (3) The growth rate of the pooled macroalgal node, r_i . This is an average growth rate for widely different macroalgal species for which there is scarce information, so we used a wide range of regularly spaced values between 0.001 and 0.05 with 1/10 000 increments. The same values were used in unfished and fishing compliance scenarios. (4) The factor by which juvenile plant growth rate, r_j , is reduced when fishers do not comply with regulation 4, i.e. leaving sparse adult plants (table 1). We used 1001 values of this reduction factor between 0 and 0.01, with 1/10 000 increments.

6. Results

Changes in the biomass of *Lessonia* kelp produced by harvesting propagated through the network of species interactions in a manner that was nearly impossible to anticipate. First, harvesting kelps well within current fishing recommendations, which dictates removing no more than 25% of the standing biomass (in our model only 20%), led to an increase in juvenile *Lessonia* plants in the kelp populations (electronic supplementary material, figure S1), which agrees well with field observations in managed kelp populations [56]. Non-compliance to the harvesting regulation dictating that some adult plants must be left standing led to extinction of the kelps, demonstrating the sensitivity of the system to this regulation (electronic supplementary material, figure S1). Detailed results on the target *Lessonia* species will be presented in a separate publication. Second, even though the removal of plant biomass was within the legal limits in the compliance scenario, significant negative impacts were observed on six species or nodes of the web (10%), and positive effects on two of them (3%), which were concentrated in herbivores and primary producers (algae) in the web (figure 3a). Although comparatively few species were

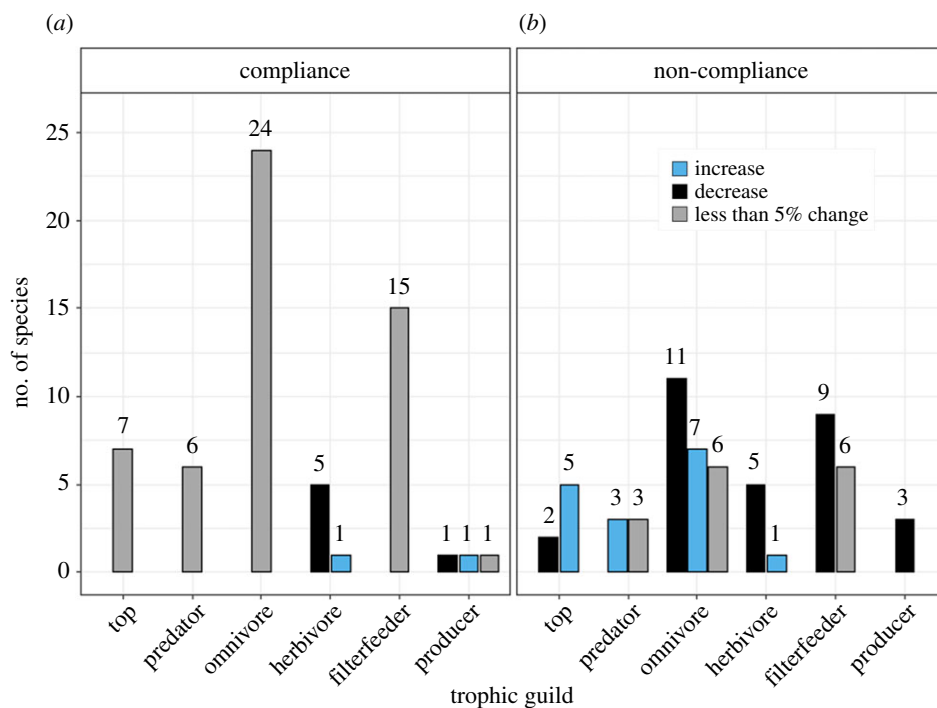


Figure 3. Number of species per trophic group that decreased (black bars), increased (blue bars) or exhibited less than 5% change (grey bars), compared to non-fishing scenario, under (a) the scenario of *Lessonia* harvesting complying with fishing regulations (compliance), or (b) not complying with regulation 4 (non-compliance, table 1).

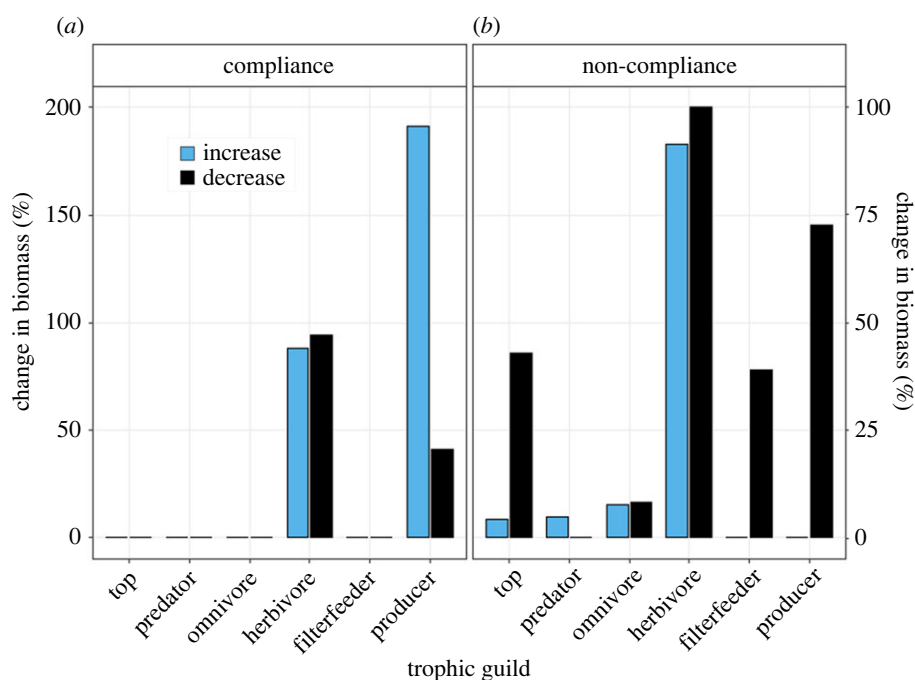


Figure 4. Changes in abundance of the rocky shore functional groups, expressed as the change in biomass with respect to the unfished scenario (no harvesting of *Lessonia* kelps). (a) Effects of fishing under the scenario of compliance to fishing regulations and (b) under non-compliance with regulation 4 (table 1). Note the different scales used for positive (left) and negative (right) changes because 100% decrease corresponds to extinction.

negatively affected by legal harvesting of *Lessonia*, biomass of those species was reduced by nearly 50%, while algal biomass was reduced by about 20% (figure 4a). These negative changes affected small-sized species that are quite abundant (littorinids), as well as small but rather rare species, like the pulmonate gastropod *Onchidella chilensis* (figure 5a). Significantly positive effects were observed in the mid-sized black

snail *Tegula atra*, which increased in abundance nearly 100% (figure 4a, 5a).

Non-compliance with the fishing regulation that some adult plants must be left standing led to different community-level changes when compared to the compliance scenario. First, 30 species were negatively affected by non-compliance to fishing regulations as compared to a non-

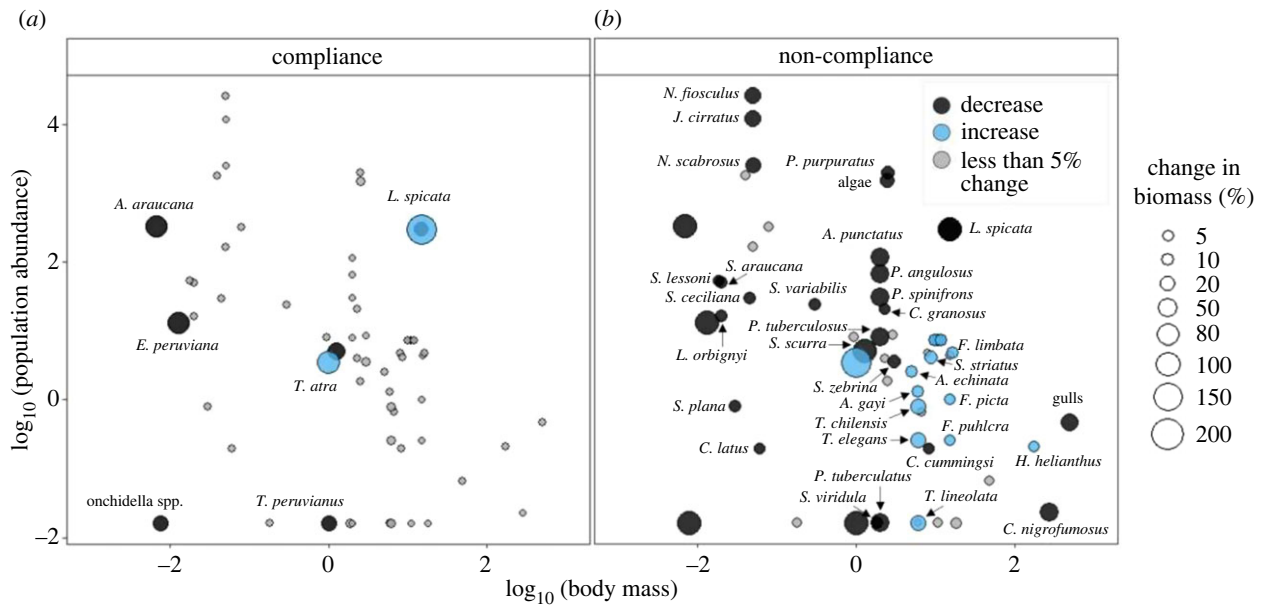


Figure 5. Summary of Allometric Trophic Network (ATN) model simulations showing the changes in the species abundances (a) after harvesting *Lessonia spicata* following all fishing recommendations (compliance) and (b) after failing to comply (non-compliance) with regulation 4 from table 1, not leaving sparse adult standing plants. The abundance of species was calculated from model results as biomass divided by the mean body mass of the species as used in the model. Changes in species abundances (diameters and point colours) are given relative to a scenario without any fishing.

fished scenario, and they were distributed across trophic groups in the ecological web (figure 3b). Of these, five herbivore species were driven to extinction (ca. 100 reduction in biomass) and many others experienced over 50% reduction in biomass (figure 4b). The types of species negatively affected were distributed all over the density–body size space, with large (greater than 50%) reductions observed in small and rare species (e.g. *Onchidella chilensis*), as well as in intermediate sized but very abundant species such as barnacles and small-sized littorinids (figure 5b). The species affected by legal fisheries were also affected by non-compliance to fishing regulations. Significantly positive effects were also observed under the non-compliance scenario and affected 16 species in different trophic groups (figure 3b), with the largest biomass increases, nearly 200%, observed in herbivores (figure 4b). Most species positively affected by illegal fishing were intermediate in body size (figure 5b). Increasing the reference level to decide whether a significant population change has occurred, from 5 to 10%, reduces the number of species responding to non-compliance fishing from 46 to 27 (electronic supplementary material, figure S2).

Qualitative results were robust to variation in fishing mortality, $F_{\max,A}$, within maximum allowable limits, as well as to variation in the rate at which plants pass from juveniles to adults, $P_{J \rightarrow A}$. This means that the same eight species significantly increased or decreased across most or all chosen parameter values and no other species were altered above the reference level (electronic supplementary material, figure S3a,b). Additional species changed more than 5% only under unrealistically low (near zero) values of $P_{J \rightarrow A}$ (electronic supplementary material, figure S3b), which may be of concern only under extremely low probability of juveniles becoming adults. Changes in growth rate of the algal node led to more changes in model response. The same eight target species responded to *Lessonia* harvesting over a wide range of algal growth rates, but some were unaltered by when algal growth rates were lower or higher (electronic

supplementary material, figure S3c). In addition to the eight core species, 14 other species (not including the algal node itself) changed in abundance, but they did so only under a very narrow range of r_j values (electronic supplementary material, figure S3c). Results were also insensitive to variation in the reduction of juvenile plant growth rate produced by non-compliance fishing, as long as the growth inhibition was very severe (electronic supplementary material, figure S3d).

7. Discussion

Monitoring all species that interact directly or indirectly in a given ecosystem through regular biodiversity assessments is unfeasible for any management agency or nation. Many of the species that participate in the transformation of biomass in the fabric of nature have attributes that make them unlikely to be included in standardized monitoring methods. Attributing biodiversity changes to management policies must be based on an understanding of species interactions. We showed that realistic models of ecological webs can be used to identify those species that will most likely respond to fishing pressure, which usually targets one or few species in the system, under scenarios of legal fishing (compliance with policies accepted by the fishery communities) and under non-compliance to those regulations. In our example, small-bodied and high or low abundance species were among those that were affected by compliant and uncompliant fisheries. Although ours is only an example and more refinements and simulations are needed in real situations, it shows that common intertidal surveys [46,66] may miss or provide only coarse estimates of abundance of this type of species. Models can help us extrapolate the effect of management to those less-documented parts of the fabric of nature. In our example, a small filter feeder and five small grazer species (see figures 4 and 5), none of them directly exploited

by humans, are candidates to be included in regional monitoring programs.

From a management perspective, it is interesting to note how our model identifies the effects of changes in policy and compliance. Indeed, the identity of species, or the direction of change in species abundance, can be altered under different management scenarios. Species that show this strong coupling to management can serve as ‘interaction-indicator’ species, which can help achieve one of the foundational goals of EBM [4,24]: ‘to link observed biodiversity changes to management policies’. Many of these indicator species may be missed or overlooked in traditional biodiversity surveys. Managers can therefore use the model results to ensure monitoring programmes include these interaction-indicator species or to design species-specific surveys to monitor their abundance, along with the implementation of management plans.

The use of multi-species or multi-component models has been advocated before as the means to provide management recommendations [37,67,68], but their utility has been questioned, especially because of the high dependency on parameter values for which we have no direct estimates. Quantitative management recommendations, such as fishery quotas or assessments of fishery mortality and viability, depend highly on these parameters. Our proposal is less affected by these limitations. First, allometric trophic network models, such as the one used here, present advantages over other multi-species or multi-component models, such as Ecosim-Ecopath [67], in terms of parameterization because reasonable estimates of critical parameters can be obtained from basic allometric bioenergetic principles [59,69]. Of course, a well-resolved (species-level) and well-parameterized Ecosim model could also be used to generate qualitative scenarios as we show here using an ATN model. Second, we use the quantitative dynamic model not to make quantitative recommendations for management, but to qualitatively examine which species could most likely be affected by different management scenarios. In our example, the same species responding negatively or positively to legally compliant kelp harvesting were affected under scenarios of non-compliance, next to many others that responded only to non-compliance fishing. Since the topological structure of the web determines the pathways of propagation of biomass and information, the identity of the species being affected by the alterations of biomass produced by harvesting seems relatively insensitive to parameter values. Our sensitivity analyses lend support to this conclusion and highlight which parameters in the model are most critical. For instance, while conclusions regarding which species to include in monitoring were insensitive to variation in *Lessonia* fishing mortality (within compliance levels) and to the rate at which juvenile plants become adults, changes in the growth rate of non-*Lessonia* algae did alter which species respond to harvesting. The same eight species responded to harvesting over a comparatively wide range of realistic algal growth values (electronic supplementary material, figure S3c), but some stopped responding to harvesting at more extreme parameter values. A precautionary approach would dictate that they must be included in monitoring. The general recommendations for managers are therefore unaltered. Conversely, few other species also responded to *Lessonia* fishing, but only under a very narrow range of algal growth rates. Managers would have to factor in the costs of including these additional species in monitoring programmes since under most conditions they will not be

altered by fisheries. Thus, sensitivity analysis can also provide a means for managers to prioritize which species to include in monitoring programmes.

It is important to emphasize that our purpose here is to illustrate the need for multi-species models in biodiversity monitoring and attributing process. Our example is part of a larger effort to model the impacts of kelp harvesting on coastal ecosystems and the model will be improved as critical field data becomes available. Perhaps the most critical shortcoming of our example is the absence of non-trophic interactions (other than space competition), which are known to deeply alter the dynamics ecological webs [60]. The general structure of the ATN model used here can accommodate different types of non-trophic interactions [60], which are fairly well documented [47] and must be included before advising specific monitoring programmes.

The extent and rate at which human activities are altering marine and terrestrial ecosystems largely surpasses our capacity to even document the diversity of life in those ecosystems [13,70]. Attributing diversity changes to specific practices is critical for conservation of biodiversity and sustainability of ecosystem services [15], yet this can rapidly become an insurmountable challenge, even in species-poor systems. Effects propagate throughout the ecological network, sometimes pushing unsuspected species to the brink of extinction. Here we show that dynamic quantitative models of ecological networks, such the ATN model, can be used in a qualitative manner to link management practices with diversity change. The long-established and worrisome dependency of these models from a large number of parameter estimates is much reduced when used for qualitative recommendations regarding monitoring programmes and the precautionary principle is followed. In this manner, managers can design and implement specific diversity monitoring programmes to include species that might be under threat, even when target species are otherwise well-managed.

Data accessibility. Simulation code and the Chilean intertidal data is available from the Github Repository: https://github.com/IsidoraAvilaThieme/Monitoring_Fabric_of_Life.

The Chilean ecological network, with trophic and non-trophic interactions, is available at <https://map.openmapp.org/chile-marine-intertidal-network/>.

The data are provided in electronic supplementary material [71].

Authors' contributions. S.A.N.: conceptualization, funding acquisition, investigation, methodology, project administration, resources, supervision, visualization, writing—original draft, writing—review and editing; M.I.A.-T.: formal analysis, investigation, methodology, writing—original draft, writing—review and editing; D.V.: data curation, formal analysis, methodology, writing—original draft, writing—review and editing; A.G.: formal analysis, investigation, methodology, writing—original draft, writing—review and editing; S.G.: funding acquisition, resources, writing—original draft, writing—review and editing.

All authors gave final approval for publication and agreed to be held accountable for the work performed therein.

Conflict of interest declaration. We declare we have no competing interests.

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