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Community-wide scan identifies fish species associated with coral reef services across the Indo-Pacific

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Determining whether many functionally complementary species or only a subset of key species are necessary to maintain ecosystem functioning and services is a critical question in community ecology and biodiversity conservation. Identifying such key species remains challenging, especially in the tropics where many species co-occur and can potentially support the same or different processes. Here, we developed a new community-wide scan (CWS) approach, analogous to the genome-wide scan, to identify fish species that significantly contribute, beyond the socio-environmental and species richness effects, to the biomass and coral cover on Indo-Pacific reefs. We found that only a limited set of species (51 out of approx. 400, approx. 13%), belonging to various functional groups and evolutionary lineages, are strongly and positively associated with fish biomass and live coral cover. Many of these species have not previously been identified as functionally important, and thus may be involved in unknown, yet important, biological mechanisms that help sustain healthy and productive coral reefs. CWS has the potential to reveal species that are key to ecosystem functioning and services and to guide management strategies as well as new experiments to decipher underlying causal ecological processes.

1. Introduction

Within the context of global changes and biodiversity loss, effective ecosystem management relies on a better understanding of the causal pathways between ecological communities and the myriad of services they sustain [1–4]. Experiments that manipulate community compositions have unambiguously demonstrated the positive effect of species diversity on ecosystem functioning over short and long time scales [5–8]. Recent studies have also convincingly shown that natural species-rich communities are more productive and can deliver higher rates of ecosystem services than impoverished communities [9,10]. Beyond the mere number of species, the diversity of species traits and evolutionary histories has been shown to promote ecosystem functioning in both controlled experiments and natural communities [11–14]. In parallel, another line of evidence suggests that particular species are key to ecosystem functioning as they contribute disproportionally to certain processes when present [15–19]. However, identifying these key species remains highly challenging in diverse ecosystems, such as tropical reefs or rainforests, where many species co-occur and can have multiple or unique contributions to ecosystem functions and services [17,20].

To tackle this challenge, ecologists can now use the increasing availability of extensive and standardized databases that have compiled environmental, social and ecological information across space and time [9,21]. This emergence of large social-ecological databases parallels what happened 20 years ago in genetics with advances in genome sequencing generating millions of genetic variants for individual loci. To identify genetic variants among this myriad of sequences that are more frequent in people with a particular disease or traits of biomedical significance, genome-wide scans or genome-wide association studies (GWAS) were developed [22]. Such an approach is powerful to relate a given biological feature or trait to its underlying genetics, based on the simple idea that if a genetic variant increases the frequency of a given trait it should be more frequent in individuals with this trait than expected by chance [23]. Although this approach does not attribute causality, it can uncover previously unsuspected, yet important, potential biological mechanisms and pathways [24]. Although similar approaches have not been used in ecology, they hold much promise in empirical community ecology where only a few, among dozens or even hundreds of species (the ecological equivalents of genetic variants) can disproportionally drive ecosystem functioning and the delivery of services (the equivalents of diseases, traits or phenotypes) [17,19,25]. This approach could also reveal the unknown level of ecological pleiotropy in communities (i.e. the propensity that a single species can be key to many ecological functions and services) [26,27]. This term was initially coined by Strauss & Irwin [28] by analogy to genetic pleiotropy, where one gene can influence two or more seemingly unrelated phenotypic traits. Under ecological pleiotropy a few species, so only a small fraction of biodiversity, may underpin many different ecosystem functions or services and would deserve particular conservation actions.

Identifying functionally important or key species is particularly challenging in biodiverse ecosystems, due largely to the complexity of interactions between species and with their environment including human disturbances. For example, despite the large body of research on coral reefs, the identification of fish species that disproportionally drive ecosystem functioning is still in its infancy [15,29]. The functional importance of most coral reef fishes is still poorly understood, and no study has scanned entire fish communities to detect potential links with ecosystem functioning and services at large scale. Here, we develop a new community-wide scan (CWS) approach, analogous to the GWAS approach, to identify key fish species that are linked to the delivery of services on coral reef ecosystems. Here 'key' has a different meaning than 'keystone', which corresponds to a 'species whose effect is large, and disproportionately large relative to its abundance' [30]. We define key species as those consistently and significantly associated (i.e. above a certain statistical threshold) to a certain level of ecosystem functioning or services.

More precisely, we propose a statistical framework and use empirical data from 1824 Indo-Pacific coral reefs hosting approximately 400 fish species to determine species whose presence is disproportionately related to fish biomass and live coral cover which insure, for instance, fisheries yield [31] and coastal protection [32], respectively. We then place those key species on a reef fish phylogeny, and in a functional trait space [33] to show the extent of species traits and evolutionary lineages that are necessary to sustain these two services on coral reefs. Identifying key species can provide new research priorities to elucidate ecological processes by which such candidate species positively affect coral reefs and to motivate a diversification of management options to maintain fish communities and their associated services in the face of a highly uncertain future.

2. Material and methods

(a) General framework

The CWS framework to identify species that are associated with higher levels of ecosystem services involves three steps (figure 1). The first is collecting environmental, socioeconomic, species presence and/or abundance, and indicators of ecosystem services data across many sites. The second step is modelling a given (or several) ecosystem service as a function of this large set of predictor variables (socioeconomic, environmental conditions and species richness). The accuracy and parsimony of this comprehensive initial, or reference, model (M0) is validated according to its R^2 and its Akaike information criterion ($\mathrm{AIC}_{\mathrm{M0}}$), respectively. The third step is testing the effect of each species separately on each ecosystem service beyond the effect of previous variables including species richness. For this, the presence of a given candidate species in a community (coded as a binary variable) is added as an explanatory variable to M0. The resulting model M1, so the importance of the candidate species to explain variations of a given ecosystem service, is evaluated according to its AIC ($\mathrm{AIC}_{\mathrm{M1k}}$). A species is declared as a potential key contributor to the ecosystem service if ΔAIC ($\mathrm{AIC}_{\mathrm{M0}} - \mathrm{AIC}_{\mathrm{M1k}}$) greater than 4 and if its partial effect is positive (figure 1).

(b) Coral reef data

(i) Coral reef services

The proxies for coral reef services we considered are fish biomass and live coral cover which support, among many others, food security, shoreline protection and recreational value [31,32,34,35]. We used data from 1824 coral reefs in 26 nations/states located across the Indo-Pacific, which include fish biomass (electronic supplementary material, figure S1) and live coral cover (electronic supplementary material, figure S2) estimates (see details in the electronic supplementary material).

(ii) Initial models and species candidates

For each of the 1824 reefs located in the Indo-Pacific we collected and used 12 relevant social and environmental variables (listed below), together with the occurrence, abundance and size of 739 reef fish species [21]. To build the initial model (M0) and estimate the reference $\mathrm{AIC}_{\mathrm{M0}}$ we modelled fish biomass and live coral cover using linear mixed models (LMMs) with the complete set of socioeconomic and environmental conditions plus species richness as predictor variables. For each of the 739 fish species present in this dataset, we estimated the number of reefs where a given fish species was present. To avoid results only influenced by a few reefs we chose to remove rare species. Rarity can be seen as a relative (compared to other species) or absolute (compared to the number of sampled reefs) concept while cutoffs are always subjective [36,37]. Here, we excluded species present on

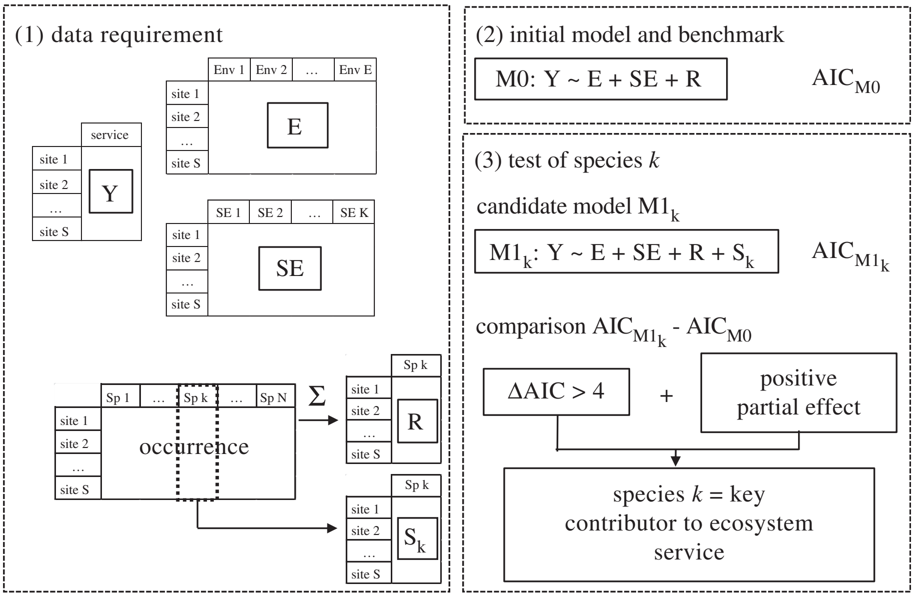

Figure 1. Statistical framework to assess the significant potential contribution of species to ecosystem services beyond the effects of environmental and socioeconomic conditions and species richness. (1) Collecting datasets: for a (large) set of sites, variables describing a given ecosystem service (Y), environmental (E) and socioeconomic conditions (SE), and the occurrence of species. Species richness (R) is computed for each site from the sites-species matrix as well as the vector (S_k) with presence–absence of each species in sites. (2) The goal is to model a given ecosystem service (Y) according to environmental (E) and socioeconomic conditions (SE) and species richness (R); to check its relevance according to its explanatory power and to save its AIC_{M0} as a reference for the next step. (3) The goal is to identify species key for the studied ecosystem service (Y) adding each candidate species (presence–absence, S_k) as an additional explanatory variable to M0 to compute model M1 and its associated AIC (AIC_{M1k}). Finally, a species is declared as a key potential contributor to the ecosystem service if ΔAIC ($AIC_{M0} - AIC_{M1k}$) > 4 and if its partial effect is positive (positive coefficient in the model).

less than 1% of the reefs (i.e. 18 and 7 reefs for fish biomass and coral cover dataset, respectively), so we retained 381 species, which corresponds to roughly half (51%) of the species pool, a conservative threshold to define rarity [36]. These 381 fish species, belonging to 116 genera and 30 families, were considered as potential candidate species.

(iii) Identifying potential key contributors to ecosystem services

Each of the 381 species was tested as candidate for improving prediction of reef fish biomass and live coral cover given the socioeconomic and environmental conditions at each study site. More precisely, we tested presence of each candidate species as an additional explanatory binary variable to M0 to compute model M1 and its associated AIC (AIC_{M1k}). Finally, a species was identified as a potential key contributor to a given ecosystem service if, when included, ΔAIC was greater than 4 and if its partial effect was positive (positive coefficient in the model). The binary variable describing the presence/absence of a species was strictly related to its occurrence in our study (i.e. presence of at least 1 individual) but could also be determined using any relative abundance threshold (figure 1; electronic supplementary material).

(iv) Environmental and socioeconomic variables

Some variables included in the models were environmental: (1) oceanic productivity, (2) habitat type, (3) depth. Others were socioeconomic: (4) management, (5) local human population growth rate, (6) gravity of local population, (7) gravity of markets, (8) levels of human development (human development index), (9) human population size, (10) levels of tourism, (11) degree of voice and accountability of citizens and (12) reef fish landings (details are provided in the electronic supplementary material).

(v) Statistical analyses

We first built two LMMs, which predicted fish biomass and live coral cover respectively, while accounting for the different scales at which the data were collected as random effects (reef site, location and nation/state, electronic supplementary material), with 12 key environmental and socioeconomic variables expected to influence reef conditions [21,38] and fish species richness as fixed effects (electronic supplementary material). To evaluate the fit of the two linear mixed models, we checked the relationship between observed and predicted values. Model validation and quality control procedures are described in the electronic supplementary material.

In order to quantify the potential net benefit of each identified key species, we extracted the net effect of each key species for biomass and live coral cover using a partial plot from linear mixed models while the other variables were held constant.

We next investigated whether reefs with several key species show high levels of fish biomass and live coral cover. To control for the effects of species richness we compared modelled estimates of fish biomass and live coral between reefs while increasing the number of key species. We estimated the number of key species present on each reef and chose the richest quartile as a threshold (i.e. four and six key species for biomass and live coral cover respectively). We next created three categories of reefs: those with no key species, those with at least one key species but below the richness threshold (four and six for biomass and live coral cover, respectively), and those with more key species than the threshold.

(vi) Functional space and entities

The 381 candidate fish species were functionally described using six traits: (1) size, (2) mobility, (3) period of activity, (4) schooling, (5) vertical position in the water column and (6) diet. Values for these six traits were taken from the global trait database on tropical reef fishes from Mouillot *et al.* [39] (electronic supplementary material). The 381 candidate species represented 240 functional entities and most functional entities comprise species from different genera [39].

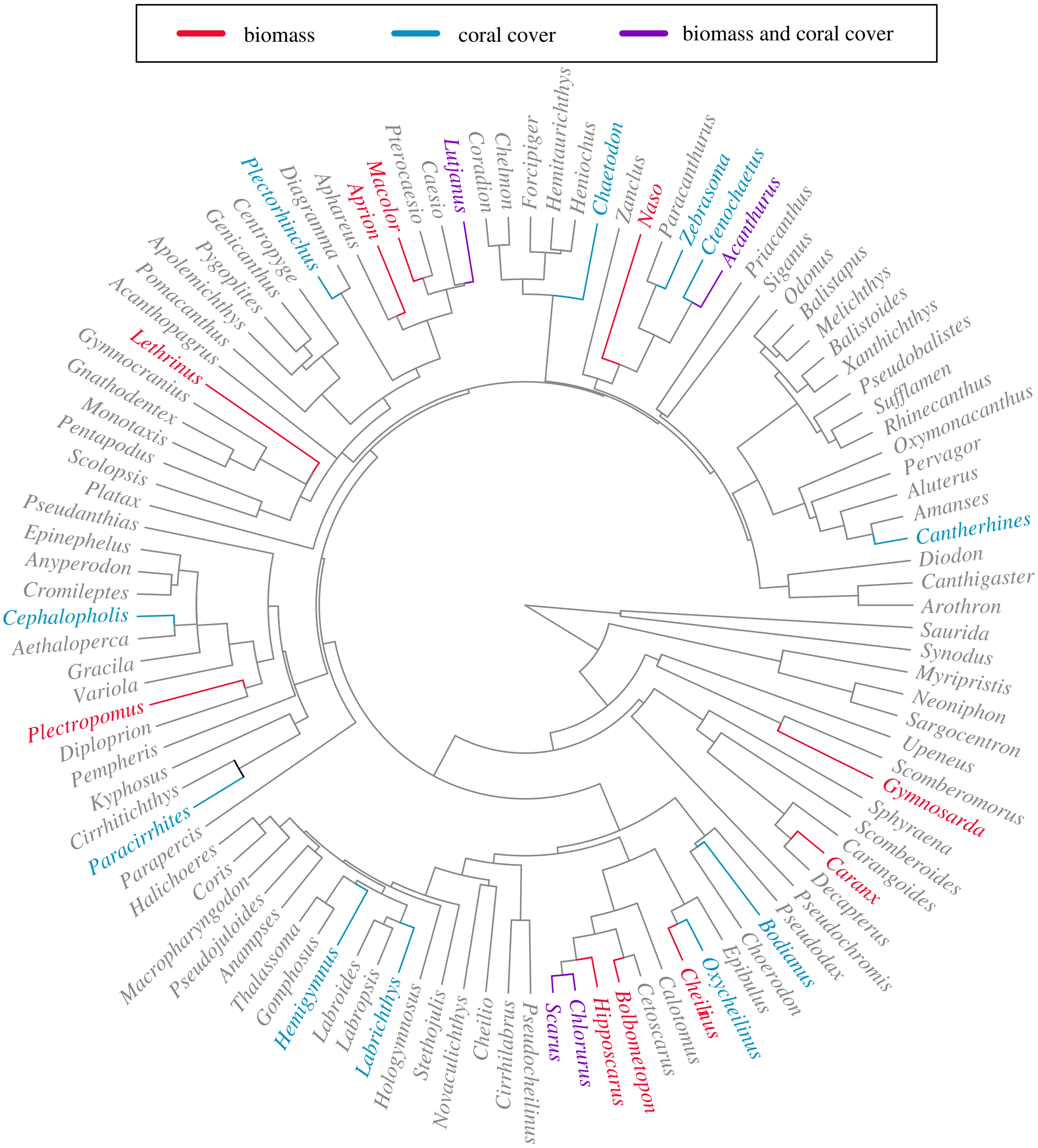

Figure 2. Positions of key species for biomass (red), live coral cover (blue) or both of them (purple) represented as their corresponding fish genera in the Tree of Life of Coral Reef Fishes, adapted from Near *et al*. [41]. The 26 key species for biomass represent 16 genera while the 28 key species for coral cover represent 15 genera with 4 common genera. *Elagatis* and *Parupeneus* genera are missing.

We assessed functional richness (FRic), the functional space occupied by the key fish species for biomass and coral cover respectively, using the convex hull volume index proposed by Cornwell *et al.* [40]. This volume corresponds to the amount of multidimensional (four in our case) functional space filled by key species, where axes are defined by species traits.

(vii) Fish phylogeny

We used a phylogeny of acanthomorph fishes [41] which covers all 30 reef fish families of the present study (electronic supplementary material, table S1). Some fish genera (e.g. *Elagatis* and *Parupeneus*) recorded on reefs were missing in this phylogeny.

3. Results

(a) Predictability of fish biomass and coral cover

The two initial (M0) models explained 79% and 61% of the variance in fish biomass and live coral cover, respectively (electronic supplementary material, figure S3). The residuals of the two models were normally distributed (electronic supplementary material, figure S3). In total, eight and six variables had the highest importance (Akaike weight = 1) in predicting fish biomass and live coral cover, respectively (electronic supplementary material, tables S2 and S3). Fish species richness, oceanic productivity, population size, tourism and census method were the main predictors of both fish biomass and coral cover. Depth, management and sampling area were also important predictors of fish biomass while habitat type was important in predicting coral cover (electronic supplementary material, tables S2 and S3).

(b) Key species associated with reef fish biomass

Among the 381 fish species considered as candidates, only 26 species (7%) were significantly related to fish biomass beyond the initial set of variables ($\Delta\text{AIC} > 4$ and positive effect), after considering their presence (at least one

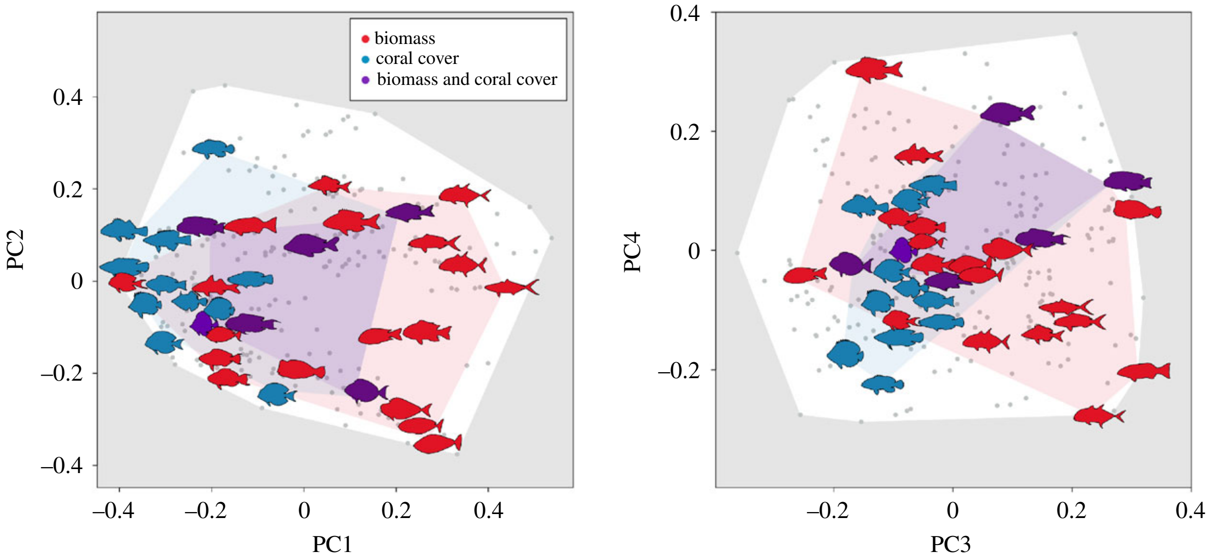

Figure 3. In total, 51 fish species which correspond to 35 out of 240 functional entities (15%) have been identified as strongly related to high biomass (18 red shapes), high live coral cover (11 blue shapes) or both of them (6 purple shapes). The positions those 35 functional entities in the four-dimensional functional space are defined according to species trait values. Fish shapes were chosen to illustrate the main genus of the species comprised in each functional entity, other functional entities are represented with grey dots. Coloured areas represent the functional volume filled by the functional entities strongly related to high biomass (red, FRic = 0.2), high live coral cover (blue, FRic = 0.05), both of them (purple, FRic = 0.01) or all functional entities (e.g. all species, white) present in the dataset.

individual; electronic supplementary material, table S4). Those 26 key species covered a wide breadth of phylogenetic lineages (figure 2), representing 16 out of 116 genera and 8 out of 30 families (i.e. Acanthuridae, Carangidae, Labridae, Lethrinidae, Lutjanidae, Mullidae, Scombridae, Serranidae).

When considering functional traits, we found that those 26 key species represented 24 different functional entities (electronic supplementary material, table S6) demonstrating a very low functional redundancy with 1.1 species per functional entity (median = 1; range: 1–2). In addition, key species had contrasting functional traits with all body sizes (from 10 cm to greater than 50 cm) and all diets (seven trophic categories) represented (electronic supplementary material, table S6). Together these 26 key species filled 20% of the whole functional space defined by the 240 functional entities corresponding to the 381 candidate species (FRic = 0.20; figure 3).

(c) Key species associated with live coral cover

We found that 28 reef fish species out of 381 (7%) were significantly and positively related to coral cover (ΔAIC > 4), after considering their presence (electronic supplementary material, table S5). Those 28 key species also encompassed a wide breadth of phylogenetic lineages (figure 2), representing 15 out of 116 genera and 8 out of 30 families (i.e. Acanthuridae, Chaetodontidae, Cirrhitidae, Haemulidae, Labridae, Lutjanidae, Monacanthidae, Serranidae).

When considering functional traits, we found that the 28 key fish species were distributed among 17 different functional entities (electronic supplementary material, table S6). Key fish species with regard to coral cover showed some degree of functional redundancy with, on average, 1.6 key species per functional entity (median = 1; range: 1–6 species). This higher functional redundancy translated into a more restricted functional space filled by these key species (only 5% with FRic = 0.05; figure 3). Species of all sizes (from 10 cm to greater than 50 cm) and almost all diets (six diet categories out of seven) were significantly associated with live coral cover. However, large mobile predators and large herbivorous fishes were not considered as key for live coral cover (electronic supplementary material, table S6).

(d) Low overlap between key species with regard to fish biomass and coral cover

The two sets of key species associated with total fish biomass and live coral cover (26 and 28 key species, respectively) each represented less than 10% of the 381 fish species tested as candidates. Only three species (*Acanthurus albipectoralis, Lutjanus bohar, Lutjanus gibbus)* were common to both sets, while four genera (*Acanthurus, Chlorurus, Lutjanus and Scarus*) and four families (Acanthuridae, Labridae, Lutjanidae and Serranidae) presented key species significantly associated with the two reef services (figure 2, electronic supplementary material, table S6).

Only six functional entities were common and significantly associated with both biomass and live coral cover (figure 3), namely small and medium herbivores, small planktivores, medium and large fishes targeting mobile invertebrates and meso-predators (electronic supplementary material, table S6).

(e) The net benefit of key species for fish biomass and live coral cover

When present, each key species belonged to a community with a median level of fish biomass higher (560 kg ha^{-1}, range: 439–773 kg ha^{-1}) than the median biomass observed when absent (370 kg ha^{-1}, range: 337–385 kg ha^{-1}). Similarly, live coral cover was estimated at a median value of 50% (range: 36–82%) when each key species was present against 34% (range: 26–38%) when absent (figure 4). For clarity, we only presented the net effect of the four most

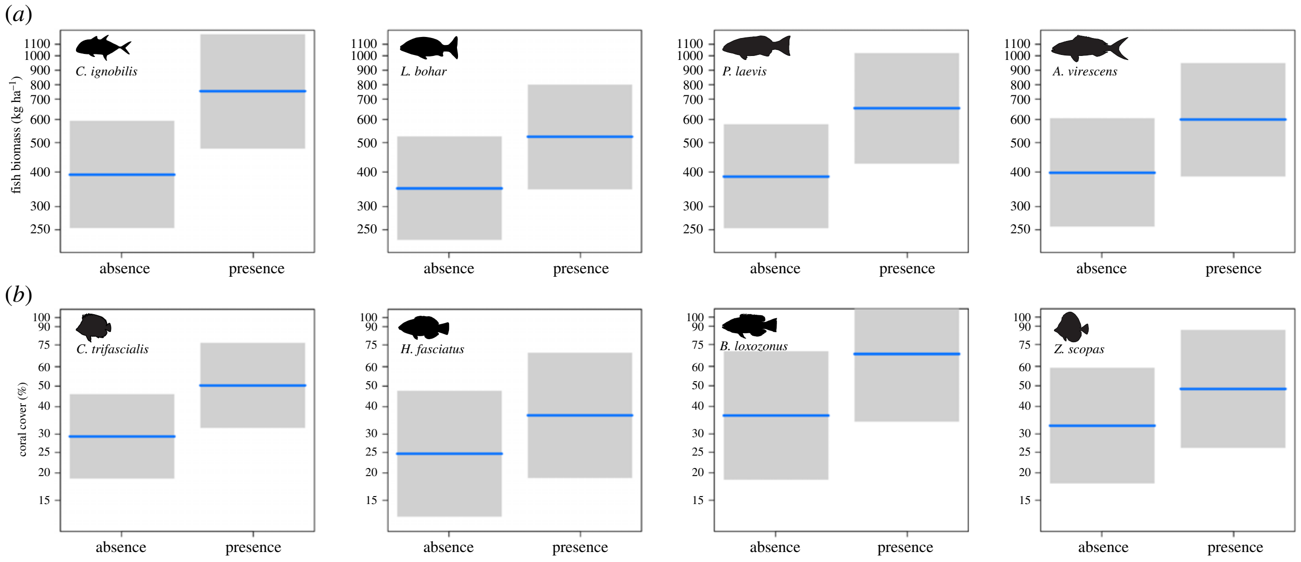

Figure 4. Net effect of the four most significant (lowest AIC) key fish species when present for (*a*) fish biomass and (*b*) live coral cover (among the 26 and 28 key species, respectively) using a partial plot from the linear mixed models while the other variables are held constant. When present, each key species is linked to a median level of biomass and live coral cover significantly ($p < 0.05$) higher than the level observed where absent. (Online version in colour.)

significant key species (lowest AIC; electronic supplementary material, tables S4 and S5) associated with biomass and live coral cover (figure 4). Importantly, these four most significant key species (lowest AIC) were not necessarily related to the highest level of biomass and coral cover (electronic supplementary material, figure S4).

It is not only individual key species, but also the accumulation of key species that was linked to high levels of ecosystem services. For instance, reefs with more than four key species reached a median level of biomass of 1150 kg ha^{-1} (range: 362–3715 kg ha^{-1}), three times the median biomass observed (370 kg ha^{-1}, range: 86–1380 kg ha^{-1}) in reefs with an intermediate number of key species (from 1 to 3 key species) and more than seven times higher than the median level of fish biomass reached in reefs having no key species (156 kg ha^{-1}, range: 12–812 kg ha^{-1}). Although less pronounced, reefs with at least six key fish species showed a median live coral cover of 40% (range: 20–68%) while reefs with no key species had a median level of 31% (range: 18–54%) live coral cover (figure 5).

4. Discussion

(a) Sustaining healthy and productive coral reefs

Even if the purpose of the present study was not to disentangle effects of anthropogenic, environmental and biodiversity drivers on fish biomass and coral cover, we found results consistent (electronic supplementary material, tables S2 and S3) with previous large-scale studies highlighting the primary importance of human density, species richness and ocean productivity on fish biomass and coral cover [42–44].

In the present study, many different fish species (approx. 400 candidate species) were scanned, and only 26 and 28 species were identified as significantly and positively related to fish biomass and live coral cover, respectively, with only three species being common to both. In total, these 51 species (i.e. approx. 13% of the species pool tested) represent 35 distinct functional entities (out of 240, i.e. 15%) that are widespread in the functional space. While large-bodied species may be expected to disproportionately contribute to fish biomass, our results indicate that only 25% (7 out of 26; electronic supplementary material, table S6) of key species for fish biomass were large-bodied (greater than 50 cm), which is directly comparable with the percentage of large-bodied species among the initial candidate species (24% or 91 fish species out of 381). In addition, 35% of key species for fish biomass were smaller than 30 cm (9 out of 26; electronic supplementary material, table S6). The positive association with fish biomass is thus independent of body size.

It comes as no surprise that some key fish species identified in this study have already attracted considerable interest in coral reef ecology. Herbivorous fish support coral reef resilience by preventing coral–algal phase shifts [17,45–49], and therefore may contribute to the maintenance of high coral cover and fish biomass. In particular, scarine parrotfishes (i.e. *Bolbometopon*, *Chlorurus*, *Hipposcarus* and *Scarus*; electronic supplementary material, tables S4–S6) play critical roles as grazers and bioeroders of the reef substratum [50,51], and their abundances have strong positive effects on cover of corals and hence accretion rates of the reef [52]. Further, grazing and detritivorous acanthurids (i.e. *Acanthurus* and *Ctenochaetus*; electronic supplementary material, tables S4–S6) intensely graze epilithic algal turfs [48,53], while benthic-feeding unicornfishes (i.e. *Naso*; electronic supplementary material, tables S4 and S6) play a significant role in macroalgal removal [29,54].

By contrast, some key species identified in the present study have not previously been identified as playing significant roles. While predation is a key process shaping prey behaviour and populations [55], structuring ecological communities [56] and promoting nutrient capacity [57], no individual predator species have been expressly identified. Here, we show that predatory species like *Aprion*, *Caranx*, *Cephalopholis*, *Elagatis*, *Gymnosarda*, *Lethrinus*, *Lutjanus*, *Oxycheilinus* and *Plectropomus* (figure 4; electronic supplementary material, tables S4 and S5) may play a critical role for fish biomass and live coral cover, although the exact pathways through which they act remain to be elucidated.

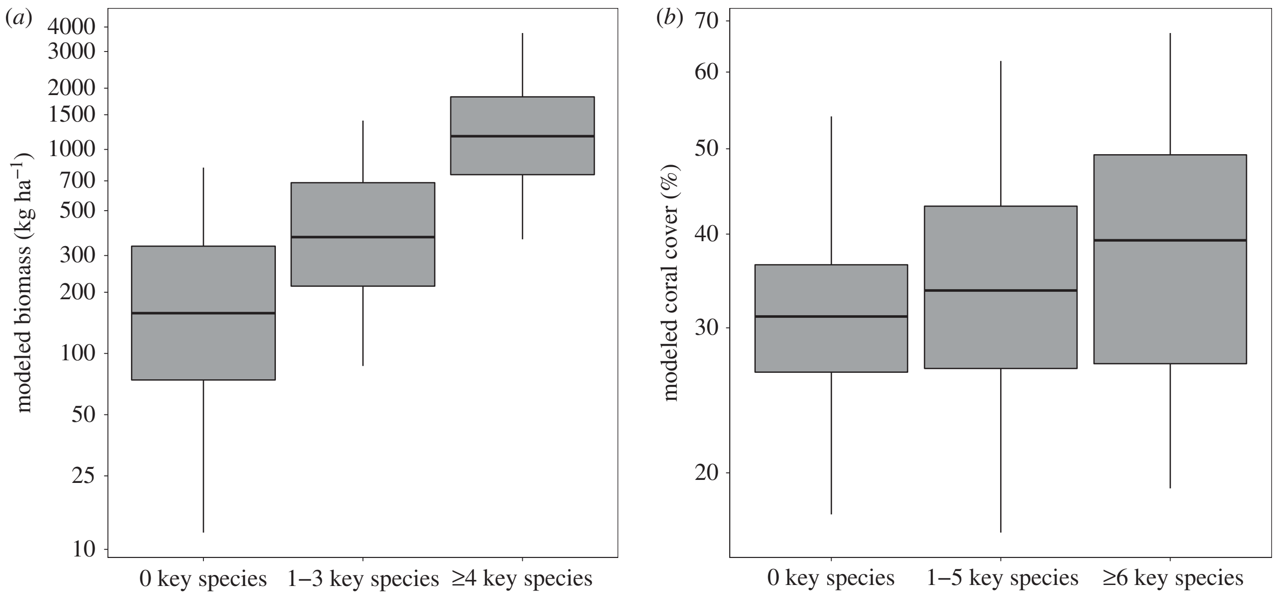

Figure 5. The accumulation of key species co-occurring on coral reefs is positively related to (*a*) fish biomass and (*b*) live coral cover. To control for positive effect of species richness on ecosystem functioning, we compared modelled estimates of fish biomass and live coral between reefs while increasing the number of co-occurring key species. Reef with the highest number of co-occurring key species reached higher levels of biomass (1150 kg ha^{-1}) and coral cover (40%) than their counterparts having no key species (156 kg ha^{-1}, 31%, respectively). Distributions are represented using 95% confidence intervals.

(b) Low ecological pleiotropy on coral reefs

The finding that a limited number of functionally and evolutionary different species are positively related to high levels of fish biomass and coral cover (figures 2 and 3; electronic supplementary material S4) supports the idea that sustaining ecosystem services may require a large breadth of particular attributes beyond the number of species [14,58]. The limited overlap between the two sets of species significantly associated with two reef services (three species, four genera and six functional entities) suggests a low level of ecological pleiotropy [28] (i.e. that a single species, genus or functional entity cannot be key to many independent ecosystem functions and services). Extended to the community level, we show that ecological pleiotropy, the opposite of functional redundancy, is not the norm on coral reefs. This finding may explain why the multi-functionality of ecosystems relies more strongly on biodiversity than do single functions [6,14,58,59], because some species play unique and thus irreplaceable roles in ecosystems [25,60]. However, it is important to keep in mind that the results may change depending on which traits and functions are considered in the analysis, and a number of yet unknown but relevant traits or functions not considered here could be included in future studies. We suggest that this ecological pleiotropy reconciles two opposing views in biodiversity and ecosystem functioning (BEF) research because many complementary species groups and lineages, and hence a large amount of biodiversity, are necessary to sustain ecosystem multi-functionality and associated services. Rather than providing multiple functions individually, those key species appear to provide high benefits in terms of fish biomass and live coral cover once combined (figure 5). Maintaining habitat heterogeneity and high regional species diversity is thus a major component of management and conservation. Our results call for more species-focused management strategies such as the banning of fishing species considered as key for the ecosystem [17]. Additionally, sustaining multi-functionality also requires a broader portfolio approach, which may reduce local extinction risk by securing the biodiversity level in an increasingly uncertain future [61].

(c) Community-wide scan as a flexible framework to link biodiversity to ecosystem functioning and services

The CWS approach can be adapted for a wide range of ecosystems, combinations of taxa or interactions and services. Here, we only tested the presence of key species, while it would be possible to look for key species groups (pairs or more), key evolutionary lineages or even key biotic interactions. Since those interactions are potentially multiple in species-rich communities they cannot be experimentally tested but they can emerge from empirical data using the CWS approach. The way candidates are tested can be modified while respecting independence between predicted and explanatory variables. As positive effects of some species may only be revealed beyond particular thresholds, presence data can also be determined by any abundance threshold such as a minimum number of individuals, cover rate, biomass or level of interactions.

On coral reefs, defining species presence based on distribution of its biomass across study area (using upper percentiles or deciles) can promote the inclusion of small-bodied species but can also discriminate against species that are not commonly encountered or have skewed biomass distributions (electronic supplementary material, tables S7–S10). Rather, defining species presence according to its relative biomass in communities can be applied independently of the species biomass distribution. However, we found consistent results between these two procedures because the majority of species detected as key species using the intracommunity approach are also significant using the intraspecific approach, reinforcing the robustness of our findings.

CWS studies can also be considered as initial forays into a better understanding of the complex relationships between particular species, species groups or interactions and ecosystem processes or services. Some false-positives, species being detected as key while they are not, may be revealed. Furthermore, no causality is determined in this approach; the main merit is to identify unsuspected and statistically significant positive associations. The logical progression would be to conduct experiments focusing on potential key species with the ultimate aim of highlighting the underlying ecological or biological processes that potentially sustain healthy and productive ecosystems.

5. Conclusion

The CWS approach has the potential to reveal unsuspected contributions to ecosystem functioning and its associated services, especially in complex and biodiverse ecosystems where the detection of such contributions remains challenging. The CWS approach holds much promise in empirical BEF studies where only a few species, functional or phylogenetic groups, can disproportionally drive ecosystem functioning and the delivery of services. Our framework offers a new and flexible way to analyse the ongoing massive empirical data relating biodiversity to ecosystem functioning and services with the potential to reconcile two opposing views: species identity versus diversity. Given the growing interest in the assessment and consequences of the ongoing extinction crisis on ecosystem functioning, such a framework is extremely timely and widely applicable.

Ethics. The study procedures were approved by the Institutional Review Board at the University of Montpellier.

Data accessibility. Fish biomass and coral cover dataset, fish presence and fish functional traits on Dryad: http://dx.doi.org/10.5061/dryad.45dc7qj [62].

Authors' contributions. E.M., S.V., N.A.J.G. and D.M. conceived the study; E.M. developed and ran the analyses, and wrote the first draft of the manuscript; and all the authors made substantial contributions.

Competing interests. The authors declare no competing interests.

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