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MARK JOHNSON, JESSICA FERREIRA

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Traits and metabolic constraints affect marine animal forest structure

Mark Peter JOHNSON and Jessica Afonso FERREIRA

Ryan Institute and School of Natural Sciences, University of Galway, University Road, Galway, Ireland, H91 TK33

Corresponding author: Mark Peter JOHNSON; mark.johnson@universityofgalway.ie

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Abstract

The term marine animal forests (MAFs) describes a diverse range of 3-dimensional habitats dominated by benthic suspension feeders. The ecosystem functions of MAFs are broadly understood, but an overall framework remains to be developed. We present an equation that generalizes the relationships among species' height, depth of occurrence and mean water temperature in terms of the metabolic theory of ecology (MTE). The applicability of the equation to field observations collated from the literature ($n = 284$) was tested using a multiple regression of colony density (\log of numbers m^{-2}) against transformed depth, height and temperature as predictors. Morphology was also examined both as a factor and when interacting with the effect of colony height. The model explained 39.7% of the variability in colony density with significant effects of morphology and height. Colony density decreased with taller individuals (slope -0.760 , SE 0.1677). Typical mass-height scaling in MAF species suggests that the observed slope is less than the slope that would be predicted by the MTE. A detailed evaluation requires further estimates of metabolic rates in MAF species. Some morphologies, particularly planar and bushy sea rods, reach higher colony densities than expected for their size. These morphologies have been associated with environments where food supply may be higher due to currents or turbidity. Morphology-environment associations may therefore allow traits to be incorporated into an overall description of MAF ecosystems. With further improvements in observations of both colony density and metabolic scaling with size, a comprehensive description of energy flow in MAFs could be possible.

Keywords: gorgonian; sponge; energy; crowding; morphology; size.

Introduction

Marine animal forests (MAFs) are benthic ecosystems dominated by suspension feeders like sponges and corals. Examples of marine animal forests are found throughout the oceans, are subject to a variety of threats, but remain understudied (Rossi *et al.*, 2022). The Oslo-Paris (OSPAR) Commission has highlighted 18 threatened or declining habitats, including several that overlap with MAFs: coral gardens, deep-sea sponge aggregations and sea-pen and burrowing megafauna communities (OSPAR Commission, 2008). A feature of MAFs is the formation of three-dimensional structure by the habitat-forming species. This increases the capacity for removing suspended material from the water column relative to a flat seabed, and can provide habitat, including nursery areas, for other species (Gomes-Pereira *et al.*, 2017; Francis *et al.*, 2024). Suspension feeders can alter the hydrodynamics of the benthic boundary layer and/or change the biological processing of particulate material, resulting in localized changes to sediment composition and biodiver-

sity when compared to habitat without MAF organisms (Cerrano *et al.*, 2010). Some habitat-forming species may reach ages over 100 years old (Teixidó *et al.*, 2011) and may therefore represent longer term carbon sinks. The net sequestration associated with growth of three gorgonian species has been estimated as $1.15 \times 10^{-2} \text{ t C ha}^{-1} \text{ year}^{-1}$, although there are several uncertainties associated with this estimate (Coppari *et al.*, 2019).

The use of the term 'forest' implies a scale and functional identity analogous to terrestrial forests (Rossi *et al.*, 2017). Broad scale comparative functional characterisations for MAFs have yet to be developed. For example, there is currently no MAF equivalent of the leaf area index (LAI) as a determinant of ecosystem function (Parker, 2020). While some density-size relationships have been identified for MAF-forming species (Linares *et al.*, 2008; Rossi *et al.*, 2012; Cau *et al.*, 2016) these are yet to be incorporated into a broader framework, as is common for forest plots (e.g., Ouyang *et al.*, 2019). These existing intraspecific density-size relationships in MAF species suggest that resource competition can oc-

cur, with individual size decreasing as density increases.

An overarching framework for considering the density and size relationship in MAFs is provided by the metabolic theory of ecology (MTE; Brown *et al.*, 2004). Metabolic theory is grounded in observations of the change in metabolic rates with organism size and the relationship between metabolic rate and temperature. The relationship between metabolic rate and size is known as Kleiber's law (Kleiber, 1932). Although the mechanisms and value of the scaling exponent are still debated, metabolic rate is often found to scale with body mass to the power of $3/4$. The consequence of this is that larger organisms have a lower mass-specific metabolic rate than smaller organisms. Description of the temperature dependence of metabolism is based on the Arrhenius equation for the temperature dependence of reaction rates. In most cases, reaction rates increase non-linearly with temperature and this translates to observations of metabolic rate (e.g., Gillooly *et al.*, 2001). The MTE seeks to develop predictions based on the scaling of metabolic rate with body mass and temperature. For example, Brown *et al.* (2004) describe how the carrying capacity (as density of individuals per unit area, K) is predicted to be a function of the resource supply rate (R), body mass (M) and temperature (T); with the latter two variables controlling individual metabolic rate:

$$K \propto [R]M^{-3/4}e^{E/kT} \quad [1]$$

In this relationship, the temperature dependence is defined by k , Boltzman's constant, and E , the average activation energy of metabolism (in units of eV). It is assumed that the resource supply available from the plankton and other suspended particles arriving at a MAF habitat is independent of the local population size. Equation 1 effectively divides the resource availability per unit area by the metabolic needs per individual to derive the expected population density. With the values of exponents expected from metabolic theory the predictions are that larger species will occur at lower densities, and that density will also decrease in warmer waters (i.e., at smaller values of E/kT).

A factor that may change the resource supply rate (R) for suspension feeders is depth. Concentrations of particles are likely to decline away from the photic zone due to consumption and decomposition. Observations from sediment traps demonstrate exponential declines in particulate flux with depth (e.g., Martin *et al.*, 1987). This decline in resource supply rate can be incorporated into the predicted carrying capacity as:

$$K \propto D^b M^{-3/4} e^{E/kT} \quad [2]$$

Where D is the depth of the MAF habitat and b is the rate constant for the decline in particle flux with depth.

Height is a more commonly measured characteristic of MAF-forming species than mass. As mass can generally be related to height using an allometric relationship, the predicted relationship from equation 1 should exist if height is used as a measure of organism size, although

the exponent will change. The relationship is also only expected for species where individuals can be clearly separated into free standing colonies like coral fans. Species that grow as continuous horizontal cover, while still considered MAF species, are not likely to have consistent height-mass relationships.

If different morphological classes have different height-mass relationships, this will result in different slopes for these classes in equation 2 (as the biomass-height allometry differs between groups). Such a relationship would lead to an interaction between mass (M) and morphological class as predictors of carrying capacity. The trait of morphological class may also indicate different efficiencies at extracting resources from the water column and/or different morphologies being associated with different environmental conditions (including different levels of resource availability). Different levels of resource availability by morphological class for an equivalent depth, height and temperature would change the effective value of R . We therefore tested the hypotheses that colony height, environmental temperature and depth would be related to MAF species density, with morphological class as an additional explanatory variable.

Methods

Observations of MAF species' density (number of separate colonies m^{-2}) and average colony height were collated from the literature (Ferreira & Johnson, 2025). Searches were carried out in the Web of Science using 'coral* and densit* and height*' and 'sponge* and densit* and height*' as topic searches (i.e., searches of title, abstract and keywords for each article). Articles were screened for cases where observations of habitat-forming species height and density were recorded. Papers were excluded where there was insufficient information on taxonomy (e.g., species lumped as gorgonians or soft corals), where height classes rather than mean heights were given (or mean heights and densities were otherwise unstated), and, most commonly, where the height and density terms did not reflect measurements on MAF species (e.g., a study of relationships between coral reef heights and fish densities, or studies of coral reef effects on wave height). The initial screening resulted in 33/209 papers for 'coral* and densit* and height*' and 5/111 papers for 'sponge* and densit* and height*'. There were 3 papers that occurred in both lists. The search terms 'sponge' and 'coral' are broad and may not reflect how authors describe habitats formed by free standing colonies. A greater level of detail in taxonomic categories using either common or scientific name was used to make more targeted searches: gorgonian, Alcyonacea, black coral, Antipatharia, glass sponge, Hexactinellid, sea pen, Pennatulacea. In addition, papers that used terms "sponge garden" or "sea pen field" were screened to see if density and height information were reported. The data are global, but records from around the Mediterranean and Caribbean are the most heavily represented. This pattern presumably reflects the presence of long-established marine biological research

communities. Species names in the final database of 39 papers were updated where necessary using the WORMS taxonomic database (WORMS Editorial Board, 2024).

Records in the literature did not generally report an annual average bottom temperature. Conditions typical for each species were therefore generated by retrieving species records from OBIS (OBIS, 2025) using robis (Provoost & Bosch, 2022). Average depth and average annual bottom temperature (2000-2010) for each species were calculated on the basis of values for each record extracted from rasters generated by Bio-ORACLE (Tyberghein *et al.*, 2012; Assis *et al.*, 2024).

Following substitution of mass by height (H), exponents for the terms in equation 2 were estimated by fitting a linear model in R (R Core Team, 2024) to logged densities, using logged height and temperature (as $1/kT$) for predictors. Taking logs of equation 2 makes the height, temperature and depth terms additive in a form suitable for a regression model:

$$\ln(K) \propto b.\ln(D) + m.\ln(H) + \frac{E}{kT} \quad [3]$$

Where b describes the rate of change in resource with depth, m is the scaling exponent for metabolic rate with average height, and the activation energy, E , is estimated as the slope coefficient of $1/kT$. Morphological classes for different MAF species were assigned using an existing categorization of shapes (Santavy *et al.*, 2013; Table 1). The effect of morphology was hypothesized to change the intercept of the linearized relationship and/or the interaction with height (due to intergroup variation in mass-height scaling). Morphology was therefore added as a fixed factor in the linear regression model or as a term interacting with height. The fitted linear model was not adjusted for phylogenetic covariance as a detailed phylogeny was not available across all species.

The exponents for the effects of height, depth and inversed temperature ($1/kT$) were estimated directly in the linear regression model. Changes in intercept associated with morphology compare the means for different classes, with the potential for different slopes by morphology tested with the height x morphological class interaction. The main patterns in the data can be shown using partial residual plots, which allow the effects of chosen predictors to be examined while controlling for the influence of other variables. Partial residuals were generated using the ‘effects’ package in R (Fox & Weisberg, 2018, 2019).

Results

Data ($n = 284$) were gathered across densities from 0.003 to 425 colonies m^{-2} (mean 18.4 m^{-2}), ranging from inferred temperatures of -0.6 to 23.9°C, and a depth range from 32 to 3559 m. Higher densities were associated with shorter colonies as predicted by the MTE (Fig. 1; Table 2). While the slopes for depth and inverse temperature are consistent with the hypothesized decline in densities with depth and warmer temperatures, there is not enough evidence to support these variables as predictors.

There was clear evidence for density differences among morphological classes. Including an interaction term did not improve the model fit [$\Delta AICc$ 17.2, $\ln(\text{height}) \times \text{morphology}$ interaction term not significant $F_{10,256} = 0.614$]. Many morphologies were not well represented, which limits the discrimination possible in the data. The most frequent morphological classes were bushy (SRbush), branched (SRbr) and planar sea rods (SRpl). Tukey tests ($p < 0.05$) identified the differences between these groups as $SRpl > SRbush > SRbr$. Planar sea rods had the highest mean density for an equivalent height compared to all other morphologies.

Table 1. Morphological categories used in model fitting, based on the sponge and coral categories from Santavy *et al.* (2013). ‘Varied’ and ‘other’ are used for cases where a taxon contains more than one morphological class or where a taxon is not covered by Santavy *et al.* (2013).

Category name	Abbreviation	Example taxon
Barrel	Barrel	<i>Rhabdocalyptus dawsoni</i>
Branched ropey	Bropey	<i>Farrea occa</i>
Sea rod bushy	Bushy	<i>Eunicea flexuosa</i>
Globe	Globe	<i>Sarcotragus foetidus</i>
Mound	Mound	<i>Pachastrella monilifera</i>
Other	Other	<i>Pentapora fascialis</i>
Sea fan planar	SFpl	<i>Gorgonia ventalina</i>
Sea plume	SP	<i>Antillogorgia americana</i>
Sea rod branched	SRbr	<i>Plexaurella nutans</i>
Sea rod bushy	SRbush	<i>Antipathes galapagensis</i>
Sea rod planar	SRpl	<i>Eunicella cavolini</i>
Sea rod unbranched	SRunbr	<i>Briareum asbestinum</i>
Sea whip branched	SWbr	<i>Pterogorgia citrina</i>
Varied	Varied	Isididae
Vase	Vase	<i>Asconema setubalense</i>

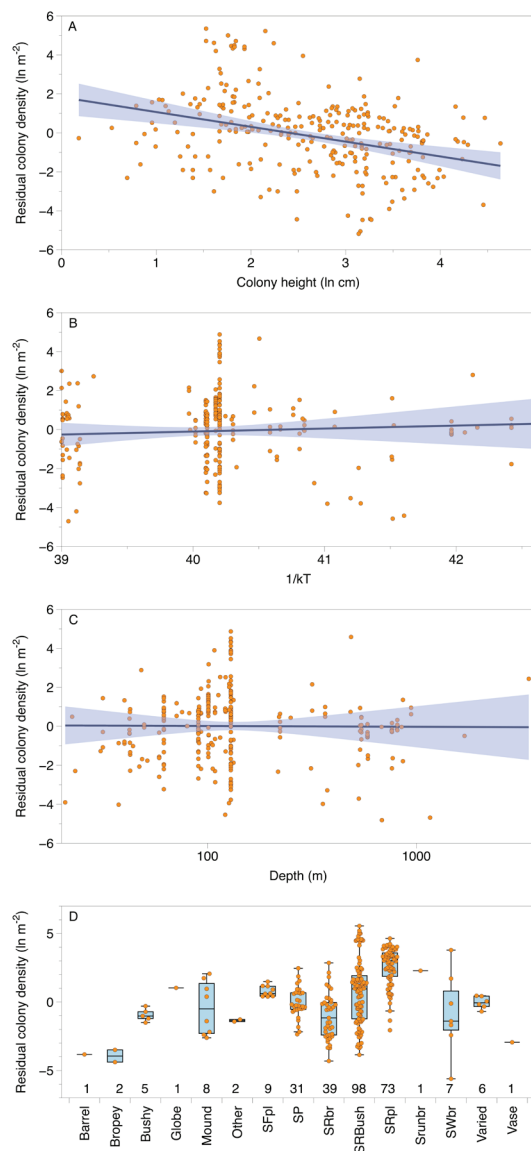


Fig. 1: Partial residual plots for the influence of A) log colony height, B) inverted temperature ($1/kT$), C) depth and D) morphological class on log colony density m^{-2} . Lines are fitted estimates (with shaded 95% confidence intervals) from the model in Table 2. The cluster of points just above 40 eV in panel B represents temperatures of approximately 16° C, with a less well-defined cluster of data at approximately 24° C on the left side of the same plot. The morphological abbreviations (described in Table 1) are labelled with the number of observations in each group. Boxes contain the median and interquartile ranges.

Table 2. Analysis of variance for $\ln(\text{colony density}, m^{-2})$ as the dependent variable with $1/kT$, $\ln(\text{colony height, cm})$, $\ln(\text{depth})$ and morphological class (morph) as predictors. k is Boltzmann's constant, T is the temperature in Kelvin. Estimated slope values are shown for the continuous predictors included in the model. Adjusted- r^2 for the model was 39.7%, AICc = 1174.41. Variance inflation statistics do not suggest strong covariance between predictors.

Predictor	Estimate (SE)	Df	MS	F	p
$\ln(\text{height})$	-0.760 (0.1677)	1	158.828	46.777	<0.001
$1/kT$	0.153 (0.2587)	1	1.955	0.576	0.4487
$\ln(\text{depth})$	-0.18 (0.2599)	1	0.016	0.005	0.9454
Morph	-	14	37.859	11.150	<0.001
Residuals	-	266	3.395		
Variance inflation (VIF)					
$\ln(\text{height})$	1.349				
$1/kT$	1.989				
$\ln(\text{depth})$	2.043				
Morph	1.046				

Discussion

The observed patterns are consistent with resource constraints on the biomass of marine animal forests in the form of a trade-off between mean size and density of colonies. A negative relationship between density and size is a prediction of the metabolic theory of ecology. Further constraints on density related to depth and temperature, as expressed in equation 2, are not supported by the data. However, the best estimates of slopes are consistent with model predictions of resources declining with depth and metabolic rates increasing with temperature.

The results observed should be considered in the light of data limitations. Data collected from the literature will contain many sources of variability, and the bias of records to shallower depths and two temperature bands probably limits the power for resolving broad scale gradients. Researchers use a variety of techniques and equipment for quantifying MAF structure, meaning that publications do not reference a standardized method. Equation 2 assumes that researchers' measurements of height and density averages have approximated the carrying capacity of species. There may be unobserved ecological processes of disturbance and recovery that have probably increased the observed variance in MAF densities and heights. Other unobserved variables are also likely to have increased the dispersion of recorded heights and densities, including local variations in topography, currents, particle supply and particle quality. Records from OBIS may not represent the environmental envelope where a taxon is found due to incomplete and uneven coverage across many species' ranges. On the other hand, populations surveyed for height and density may also be the basis for records in global databases, so the OBIS locations may reflect the conditions of surveyed populations more faithfully than the records represent the conditions across each species' range. Temperature and depth values in the Bio-ORACLE data are means for 0.05 degree cells, so may not reflect the local conditions experienced by MAF species. More detailed field studies are probably required to provide data to refute or reconsider the effects of depth and temperature given the unexplained variability around the fitted model (adj- r^2 39.7%).

The estimate of slope for the height effect in the fitted model (-0.760) is close to the value that would be predicted by a Kleiber's law exponent (-0.75). A direct comparison of coefficient is not appropriate for the current study, however, as height is used as a proxy for biomass. An interpretation of the change in colony density as a function of height in terms of MTE requires a conversion of the predictor to body mass. Such a conversion is unfortunately difficult due to the lack of available height-biomass relationships. Gaps in the definition of marine trait relationships are common even in relatively well-studied fauna (Tyler *et al.*, 2012). The information available for MAF taxa suggests that the exponent in the relationship between mass (M) and height ($M \propto H^x$) should be between approximately 2 and 3.5 (Coma *et al.*, 1998; Murrillo *et al.*, 2018; Chimienti *et al.*, 2018a,b). Typical exponents would therefore lead to a shallower density-mass

slope than observed for height (multiplying the slope by between $\frac{1}{2}$ and $\frac{1}{3.5}$), certainly less steep than the $-\frac{3}{4}$ slope predicted in the MTE [noting that observations of slopes shallower than $-\frac{3}{4}$ are common, depending on the structure of data and when examining separate taxonomic groups or other subdivisions in datasets (e.g., Currie & Fritz, 1993; Gjoni & Glazier, 2020)].

One interpretation of a relatively shallow log-density to log-mass slope is that populations of larger species use more energy than smaller species (Isaac *et al.*, 2017; Pedersen *et al.*, 2017). Hence, populations of larger MAF species will have a greater areal demand for suspended particles and a greater energy flux. A relatively greater density of larger colonies than expected could also occur if metabolic rates increased more slowly than the Kleiber's law exponent of $\frac{3}{4}$ used in the MTE: implying that larger colonies use less energy than would be expected from conventional metabolic scaling. The population-level and individual explanations for a shallower than expected density-size slope are not mutually exclusive. Resolving the alternatives needs more information on the metabolic scaling for modular organisms typical of MAF-forming species: The measured exponents are relatively variable when compared to unitary benthic invertebrates [median mass exponent of 0.83, range 0.176 to 1.19, from 29 studies of modular (colonial) species collated by Burgess *et al.*, 2017]. Potential reasons for the broad range of metabolic scaling observed by Burgess *et al.* (2017) include methodology, environmental context, integration of modules in the colony and three-dimensional morphology.

Morphological classes differed significantly in the intercept of fitted scaling relationships. There was little evidence that the slope of the density-height relationship varied with morphological class [no evidence for a morphology \times $\ln(\text{height})$ interaction]. It could be the case that mass:height allometry varies as much within as between morphologies. This type of variability would mean that morphological class was not a good proxy for size scaling. There are currently too few observed allometric relationships published to judge the variation in mass:height allometry within and among different morphologies. While Santavy *et al.* (2013) generated digital models for different morphologies, the primary focus of their study was on surface areas, equations were not based on power laws and show overlaps in predicted surface areas at the same height for different morphologies.

Planar and bushy sea rods were found at greater densities than other morphologies in the same height range. This could occur as the species have less mass for the same height compared to other morphologies or because these two morphologies have a lower metabolic rate, so that greater biomass can be supported for the same resource in a mature population. Neither of these hypotheses seem likely from the currently available evidence. Bushy and planar growth forms are not noticeably with less mass than other morphologies of comparable sizes and differences in basal metabolic rate by morphology have not been proposed for MAF species. A further alternative is that the assumption of the relatively constant resource supply does not apply to planar and bushy sea

rods. Hence these two morphologies are found at higher densities as they grow in locations where a greater resource supply supports this. Field observations and a morphology-habitat model developed for sponges supports this kind of mechanism: as planar growth forms are associated with laminar current flow (Gori *et al.*, 2012; Schönberg, 2021) likely to increase the rate of resource supply (R) to colonies in absolute terms. Similarly, bushy growth forms have been associated with more turbid water (Schönberg, 2021), potentially raising the background availability of suspended resource and leading to higher colony densities. If the colony traits do match the delivery of resource through water flow patterns, this would help explain interspecific variation in density per unit area. Further data, including local current data, is probably required across all morphologies to test this mechanism as only 4 morphological classes in the dataset had over 10 density-height data pairs.

Depth has previously been used as a proxy for resource flux (e.g., McClain *et al.*, 2012). Depth was not supported as a resource flux proxy in the current study. If this lack of a relationship is not due to limitations in the collated data, it may be that local factors can override depth effects in MAF-forming species. For example, many MAF species can occur on vertical walls and other topographic settings where supply of suspended material may be enhanced by processes linked to internal waves and tides (Johnson *et al.*, 2013; Pearman *et al.*, 2023). Variation in local currents, particulate supply, food quality and/or other locally relevant factors may modify the resource flux and hence affect the structure of MAFs. It is not possible to add such local details to the broad-scale literature-based data collected for the current study. Local factors could be examined in more detail by mapping their variation at smaller scales and comparing this to local variations in MAF density and height.

While simple allometric relationships between population density and size are relatively common (e.g., Damuth, 1987), controlled experiments on single species have indicated where equation 1 may be an oversimplification. Schuster *et al.* (2021) studied colonies of the bryozoan *Bugula neritina* and proposed that metabolic rate might covary with resource supply. In this hypothesis, increases in metabolic rate independent of size allow more active feeding up to a point where no further efficiencies in feeding can be achieved. Although a temperature effect was not observed in the current study, it is possible that the temperature effect on metabolism is not a simple relationship. Observations of the amphipod *Gammarus insensibilis* have shown an interaction between size and temperature on metabolic rate (Shokri *et al.*, 2024; 2025). This interaction would suggest a shallower temperature slope for larger taxa than smaller taxa. A fitted term for the $\ln(\text{height}) \times 1/KT$ interaction was not significant, although the data limitations, including the clustering of temperatures within the current dataset may have made this effect hard to detect.

The macroecological approach to the structure of MAFs opens the possibility of relating density and size observations to ecosystem functions like energy flux and

turnover. Existing metabolic rates can be extrapolated to provide estimates of the resource supply needed to maintain different MAFs. With better understanding of the sources of variation in observations, further predictions may be possible for changes in forest structure and function associated with changes in resource supply or temperature. Conversely, measurements of MAF size and density can provide a measure of relative status to what might be expected under optimal conditions. Alongside more data on densities and sizes, important requirements to developing a functional framework include more information on morphologies and how selection and performance of morphotypes is related to environmental conditions (Derviche *et al.*, 2022). Collation of observations from new technologies like ROV-based photogrammetry (Rossi *et al.*, 2021) and improved understanding of causes of variation in metabolic rates are likely to provide opportunities to expand the frontiers of a trait-based approach to MAF structure.

Data accessibility: Dataset is available as Ferreira & Johnson (2025). <https://doi.org/10.5281/zenodo.15276467>. **Authors' contributions:** M.P.J.: conceptualization, formal analysis, funding acquisition, methodology, investigation, visualization, writing—original draft, writing—review and editing; J.A.F.: investigation, data curation, writing—review and editing. **Funding Acknowledgments:** Research supported by the OCEAN CITIZEN project: co-funded by the European Union, under Horizon Europe Research and Innovation programme, Grant agreement No. 101093910. Research also supported by networking within COST Action CA20102 MAF World.

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