

# On the importance of defensible resources for social evolution: Applying new techniques to a long-standing question

Arne Jungwirth<sup>1</sup>  | Paul Nührenberg<sup>2,3</sup>  | Alex Jordan<sup>2,3</sup> 

<sup>1</sup>Department of Interdisciplinary Life Sciences, Konrad Lorenz Institute of Ethology, University of Veterinary Medicine Vienna, Vienna, Austria

<sup>2</sup>Department of Collective Behaviour, Max Planck Institute of Animal Behavior, Konstanz, Germany

<sup>3</sup>Centre for the Advanced Study of Collective Behaviour, University of Konstanz, Konstanz, Germany

## Correspondence

Arne Jungwirth, Konrad Lorenz Institute of Ethology, Department of Interdisciplinary Life Sciences, University of Veterinary Medicine Vienna, Savoyenstraße 1a, 1160 Vienna, Austria.

Email: arne.jungwirth@gmx.net

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## Abstract

Cooperative behaviour often co-occurs with the defence of key resources, typically in the form of a breeding site or territory communally exploited by a group of cooperating individuals. Nevertheless, not all animals that defend resources evolve advanced forms of cooperation and sociality—many non-cooperative species occupy resources that do not differ in obvious ways from those inhabited by cooperative species. A key question is thus whether cooperation confers more subtle benefits, for example by allowing access to higher quality resources through competitive exclusion of less social rivals. In other words, it is not clear whether defensible resources are a necessary precondition for sociality or whether they also contribute to the maintenance and enhancement of cooperative societies. Here, we highlight how advances in imaging technology, machine-learning, and environmental reconstruction enable the collection of behavioural and ecological data in unparalleled quantity and quality to address this question. These new techniques are especially suited to compare small-scale differences in resource use between cooperative and non-cooperative species that share a general habitat and have similar ecologies. The lamprologine cichlids of Lake Tanganyika are a prominent example of such a system and Michael Taborsky's pioneering work on this group has done much to promote these fishes as models of social evolution. We show that habitat features indicative of increased resource quality, namely increased stone cover, are indeed associated with the distribution of cooperative cichlids—at least where these resources are relatively scarce. We thus support a point Michael Taborsky made in 1981: the evolution of cooperative behaviour among cichlids is tied to their close association with a crucial resource, the substrate in which they hide and breed. In the future, the techniques we introduce here will allow to also investigate whether this substrate is indeed more than just the necessary precondition for cooperation among fishes; in addition, they will likely find application in a wide range of research fields interested in the interplay between biotic and abiotic environmental factors.

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## KEYWORDS

group living, reconstruction, resource defence, sociality, species distribution, structure-from-motion

## 1 | INTRODUCTION

Sociality and cooperation are long-standing core interests in evolutionary biology (Wilson, 2000), due to the fact that the major evolutionary transitions that led from self-replicating macromolecules to the diversity of life we observe today all involve some form of 'social behaviour' and 'cooperation' (Szathmáry & Maynard Smith, 1995), (West et al., 2015). Additionally, one of the defining features of our own species is our ability to cooperate and our need to be social (Fehr & Rockenbach, 2004). As such, social evolution concerns such diverse academic fields as paleobiology, cancer research, economics and philosophy, as well as piquing the interest of the general public.

Much of our understanding of the evolutionary drivers behind increasing complexity in cooperative relationships and concomitant social behaviours comes from research on cooperatively breeding (and eusocial) animals (Koenig & Dickinson, 2016), (Rubenstein & Abbot, 2017). In many of these systems, cooperation revolves around the communal monopolisation and exploitation of a resource crucial for survival and reproduction (Strassmann & Queller, 2014), typically in the form of a nest or territory (Macdonald & Johnson, 2015). In fact, it has long been argued that the existence of such defensible and sharable resources is a necessary precondition for the evolution of sociality (Alexander, 1974): famously, Richard Alexander predicted that, if a eusocial vertebrate was to exist, it should be characterised by the communal defence and maintenance of a burrow in which individuals would find food and shelter; an ecological setting that was later shown to be present in the naked mole rat, the only vertebrate currently argued to be eusocial (Braude, 1997), (Zöttl et al., 2016), (Braude et al., 2020). Practically, all species in which advanced forms of cooperation have been described share and defend a crucial resource, including, but not limited to: (i) shrimps defending sponges, (ii) spiders defending communal nets, (iii) termites, hymenopterans, aphids and bark beetles defending colonies and (iv) vertebrates defending territories (see respective chapters in (Rubenstein & Abbot, 2017)). These empirical observations have been supported by formal theory, highlighting that cooperation may enhance the benefits gained from the defence and exploitation of resources to 'resolve the puzzle of cooperation' (Shen et al., 2017). In fact, implicitly or explicitly, all models on the evolution of cooperation assume some sharing of a monopolised (and thus defended) resource among the interacting individuals (Lehmann & Keller, 2006), (Nowak, 2006), (Gardner & Foster, 2008).

While the existence of a sharable and defensible resource is thus well established as a necessary precondition for the evolution of cooperation, it is far from being a sufficient explanation—many species exist in each of the groups mentioned above that did not

transition to a social and cooperative lifestyle despite also defending resources either as individuals or pairs (e.g., (Hughes et al., 2008), (Lukas & Clutton-Brock, 2012), (Cornwallis et al., 2010)). What, then, is the role of such resource defence and sharing in social evolution? Is it merely a necessity that enables other mechanisms (e.g., kin selection or reciprocity) to drive a system towards cooperation and complex sociality, kick-starting the process but not crucial past its initiation (Macdonald & Johnson, 2015)? Or do defended resources play a major role in maintaining and advancing sociality and cooperative behaviours by enabling synergistic effects between the resource and the individuals that monopolise it, for example by increasing per capita yield or excluding non-social competitors (Wilson, 2008)?

Correlational evidence points towards the latter being true. Most obviously, but also least informatively, resource size tends to correlate with group size: species with larger groups tend to be found on larger nests or in larger territories (Rubenstein & Abbot, 2017). Unfortunately, causality is very difficult to infer from these observations and it thus remains unclear whether larger nests/territories can simply support more individuals or whether larger groups are at a competitive advantage in the acquisition of high-quality resources. More interestingly, certain features of the defended resource correlate with expressions of social behaviour. For example, all bees, including solitary species, establish nests for the rearing of their offspring, but eusociality is only observed in species in which nests also serve as food stores (Wcislo & Fewell, 2017). Similarly, most wasps build nests, but only highly social species construct multi-layered colonies that ensure stable environmental conditions on their inside, further facilitated by behavioural adaptations (fanning) and ensuing division of labour (Hunt & Toth, 2017). Generally speaking, increased sociality in the form of larger group size and/or increased cooperation (but see for discussions of 'increased sociality': (Rubenstein et al., 2016), (Lukas & Clutton-Brock, 2018)) appears to provide competitive advantages in struggles for resources: highly social (and cooperative) species tend to exploit a wider range of resources with greater success (in terms of resulting biomass and/or species range) than their less social relatives (Wilson, 2008).

However, supporting experimental evidence is more difficult to gather as manipulations of sociality and/or resources are difficult in most situations, particularly because they typically entail several simultaneous changes to the systems under consideration. For example, supplemental feeding or the removal of individuals, two of the classic experimental approaches in behavioural ecology, both change not only available nutrients and competition, respectively, but also alter required foraging effort (and thus time budgets) and availability of mates (and thus reproductive opportunities), complicating inferences of causality between the quality of (or competition for) a resource and social/cooperative behaviour. Notable exceptions

include translocation experiments that showed that within a species the length for which a defended resource can be expected to be exploited (Field et al., 2010) or the availability of high-quality defendable resources (Komdeur, 1992) can have drastic effects on the expression of sociality. Importantly for the scope of this manuscript, fish have proven useful in this context, because patterns observed in correlational data can be experimentally probed: the resources defended by social species, namely anemones, corals, rocks and/or shells, can be easily manipulated and behavioural responses documented, a work pioneered by Michael Taborsky ((Taborsky & Wong, 2017), (Jordan et al., 2021); see also below and Discussion for additional details).

In his seminal 1975 book *Sociobiology*, E. O. Wilson dedicated a few pages to fish sociality, largely concentrating on their schooling behaviour (Wilson, 2000). In the introduction to the respective chapter, he noted that fish (and amphibians and reptiles) 'have not evolved cooperative nursery groups' and speculated that this was likely due to a 'lack of intelligence' ((Wilson, 2000): p. 438). Only a few years later, Taborsky & Limberger showed that this statement was erroneous (Taborsky & Limberger, 1981). What is more, Wilson viewed schooling as the pinnacle of social evolution in poikilothermic vertebrates. He thus interpreted territoriality as a hindrance to advanced sociality in poikilotherms, especially fishes ((Wilson, 2000): p. 441). The work of Michael Taborsky and others over the past five decades makes a strong argument for the opposite interpretation: fish did evolve 'cooperative nursery groups' (Taborsky & Limberger, 1981), (Taborsky, 1984), but only where they defend critical resources in the form of stable territories used for protection and reproduction (Taborsky, 2016), (Taborsky & Wong, 2017).

Here, we demonstrate that the decreasing costs of underwater cameras, combined with recent advances in machine-learning-based environmental reconstruction (Francisco et al., 2020) have the potential to rapidly increase our understanding of sociality by augmenting and expanding classic studies of resource manipulation and entailing social and cooperative responses in fishes (e.g., (Bergmüller et al., 2005), (Heg et al., 2008), (Wong, 2010), (Heg et al., 2011), (Wong & Buston, 2013), (Jordan et al., 2016)). Utilisation of these emergent technologies is no longer subject to high financial barriers and can now be achieved with consumer grade cameras and computers at relatively low-cost. Similarly, open-source code and easier access to computing clusters means that these approaches are accessible to all researchers. Whether by using underwater cameras, drone-mounted cameras, or even satellites, images can be converted into various data of interest. Once footage has been collected, there now exists a wealth of tools to extract information from it: two- and three-dimensional terrain reconstructions allow for the fast and efficient production of (topographic) maps from which various structural parameters and their interrelations can be deduced (Ferrari et al., 2016); automated image recognition allows for the collection of biological data, be it with regard to habitat features (e.g., Guano cover (LaRue et al., 2014)), species abundance (Villon et al., 2018) or individual and group behaviour (Francisco et al., 2020). Finally, the statistical toolkit to analyse these types of data is continuously

expanding, encompassing Bayesian and frequentist approaches (Perry et al., 2002), (Dormann et al., 2007), (Isaac et al., 2020), (Sillero & Barbosa, 2020).

By combining image-based habitat reconstructions with species census data, we show the utility of these new tools for the study of social evolution in Lake Tanganyika cichlids with a particular focus on the role of defendable resources (in the form of rocks used for hiding and breeding) for the distribution of social and non-social species: in allowing for the collection of large quantities of high-quality data on environmental features, species distributions and individual behaviour, image-based techniques have the potential to resolve long-standing debates in this realm (see e.g., (Dey et al., 2017) and (Taborsky et al., 2019) for a recent discussion), particularly when combined with ever increasing information on phylogenetic relationships (Ronco et al., 2020). Specifically, we test the hypothesis that distributions of cooperative species are more closely associated with increased stone cover and structural complexity than distributions of other fishes. While the data we provide here is not yet 'experimental', thus not truly allowing us to infer the causal links between defendable resources and cooperative behaviour we seek to ultimately elucidate, we provide evidence for the feasibility of the methods we use for pursuing this question. We close by discussing future avenues for research on social evolution and its link to defendable resources using modern technology in Lake Tanganyika cichlids and beyond, especially the scope for pairing observational with experimental data.

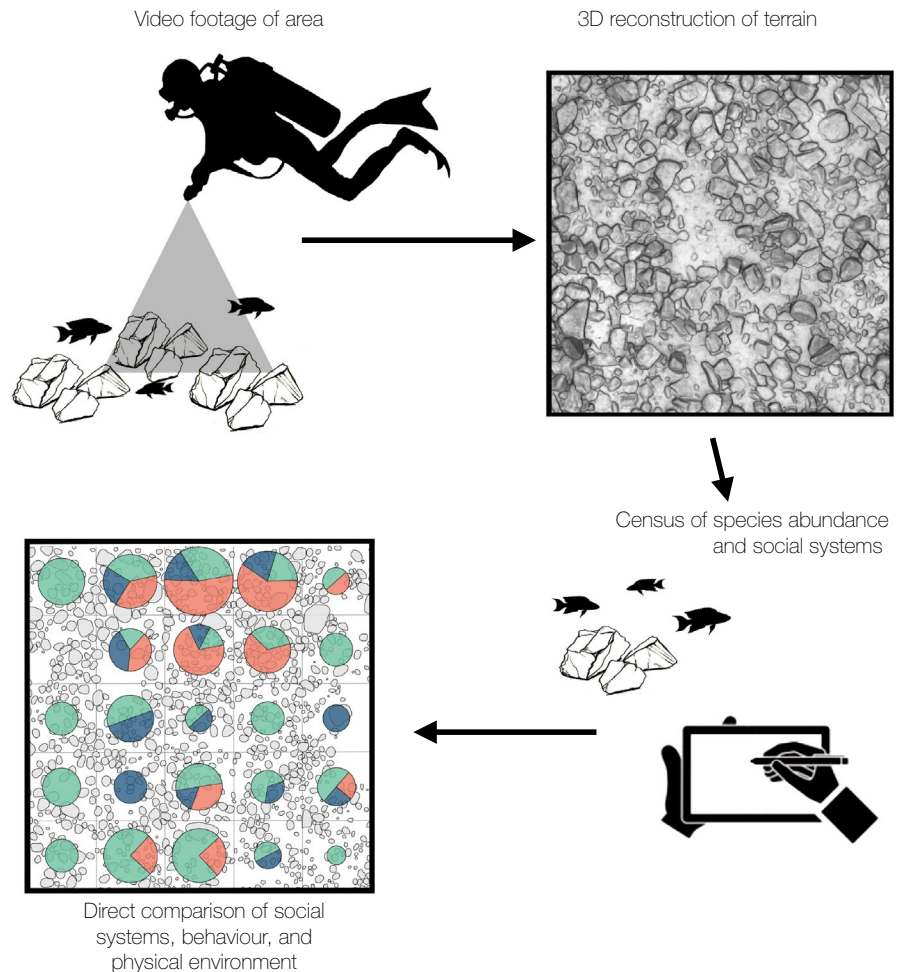
## 2 | METHODS

### 2.1 | Fieldwork—survey and filming

All works reported in this section were carried out using SCUBA (Figure 1). In September 2018, we set up three 8 × 8 m underwater plots in the southern part of Lake Tanganyika, East Africa (Figure 2). Plot 1 was located in front of Tanganyika Science Lodge at approximately 4 m depth (8°46'50"S, 31°04'51"E). Plot 2 was in the same general area, but at a greater depth of approximately 11 m (8°46'43"S, 31°04'45"E). Plot 3 was located at the south-western tip of Kumbula (Mbita) Island at approximately 7 m depth (8°45'15"S, 31°05'06"E). These plots were initially chosen in 2016 as part of a different study with an aim to include the maximum number of the following species: *Altolamprologus compressiceps*, *Eretmodus cyanostictus*, *Interochromis loockii*, *Julidochromis ornatus*, *Lepidilamprologus elongatus*, *Neolamprologus pulcher*, *Neolamprologus tetracanthus*, *Tropheus moorii*, *Telmatochromis temporalis* and *Variabilichromis moorii*. Each plot was oriented in a way that it was north-facing so that its corners were its north-eastern, south-eastern, south-western and north-western most points, respectively. Plots were then separated into grids with 1 × 1 m quadrats using white nylon string (which was recovered at the end of the observation period).

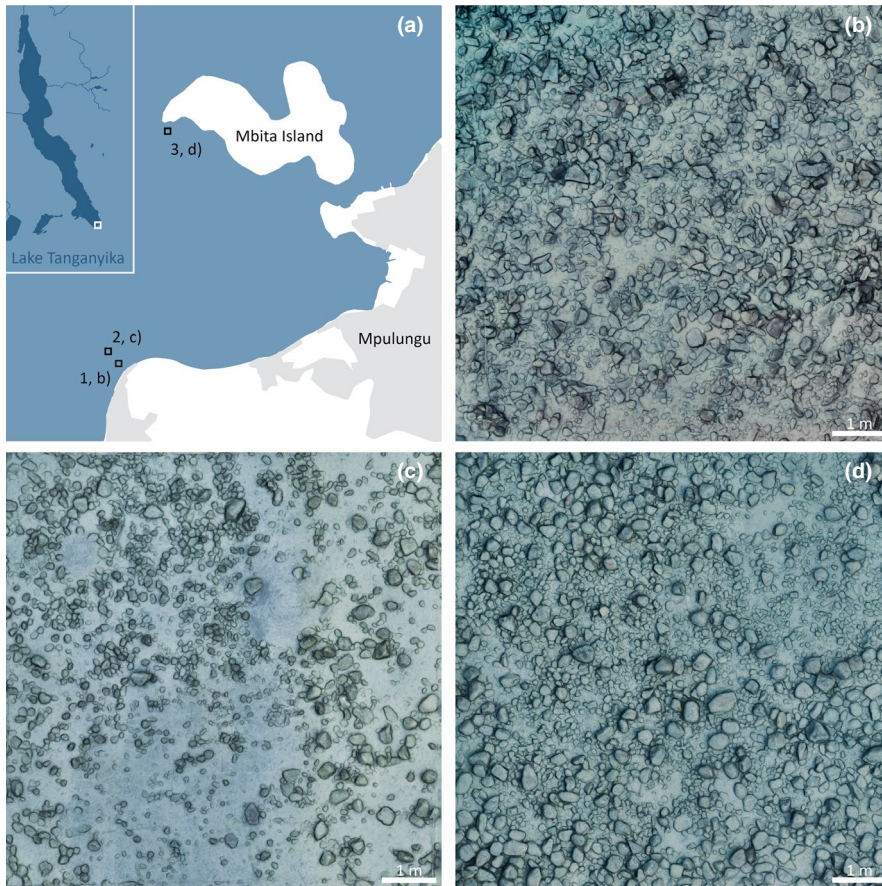
Surveys were conducted at each plot using ad libitum counts of individuals of 20 species (or families where resolution to the

**FIGURE 1** Schematic overview of the techniques reported here. Video footage and census data were recorded during field work in Lake Tanganyika, using SCUBA. Reconstructions of the terrain and all subsequent analytical steps were carried out in silico



level of species was not possible, indicated by 'spp.:' Table 1): in addition to the ten species above, we included *Lamprologus callipterus*, *Lepidiolamprologus attenuatus*, *Lepidiolamprologus lemairii*, *Mastacembelus spp.*, *Neolamprologus savoyi*, *Neolamprologus modestus*, *Ophthalmotilapia ventralis*, *Perissodus spp.*, *Telmatochromis vittatus* and *Xenotilapia spp.* These species represent a broad cross-section of fish life in Lake Tanganyika, including the whole range of trophic types from algae-grazer to piscivore (Muschick et al., 2012), (Ronco et al., 2019) and the whole range of social organisation from solitary to cooperative (Jordan et al., 2021). For many fish in Lake Tanganyika, with the exception of pelagic species and those specialising in living in sandy habitats (Konings, 1998), (Kobl Müller et al., 2004), rocks fulfil at least one of the three essential roles in a fish's life cycle: (i) they serve as the substrate on which eggs are deposited (Nagoshi, 1983), (Sefc, 2011); (ii) they provide the surface on which the primary food source grows in the form of algae and associated invertebrates (Kotrschal & Taborsky, 2010), (Ronco et al., 2019); and (iii) they form the shelters in which fish seek refuge from predation throughout their lives, from hatching into adulthood (Balshine et al., 2001), (Heg et al., 2008). In several species, snail shells fulfil the same role as rocks with regard to reproduction and protection (Sefc, 2011). Rocks and shells thus represent a crucial abiotic resource that impacts the distribution of species and the composition of fish communities at both lake-wide and local scales (Sturmbauer, Fuchs, et al., 2008),

(Takeuchi et al., 2010), (Kobl Müller et al., 2011). Within a given habitat, intra- and inter-specific competition for access to these resources is then a key factor in a fish's biotic environment for many species, often resulting in pronounced territoriality (Kohda, 1991), (Matsumoto & Kohda, 2004), (Desjardins et al., 2008), (Sturmbauer, Hahn, et al., 2008), (Winkelmann et al., 2014). We indicate the role rocks and/or shells play for each of our focal species in Table 1. Each species was scored as either 'transient' (i.e., not holding territories outside of breeding contexts), 'territorial' (i.e., permanently defending territories), or 'cooperative' (i.e., permanently defending territories and forming groups characterised by alloparental brood care; Table 1; (Kuwamura, 1986), (Sefc, 2011)). Note that the assignment of a given species to one of these categories was partly based on the geographical and temporal scales at which we collected data, that is a resolution of 1 m<sup>2</sup> and a single round of surveying. Several of the species that we consider 'transient' at this geographical scale are indeed 'territorial' at larger scales (e.g., *Neolamprologus modestus* (Hellmann et al., 2015); *Neolamprologus tetracanthus* (Matsumoto & Kohda, 2007); *Tropheus moorii* (Sturmbauer, Fuchs, et al., 2008); *Xenotilapia flavipinnis* (Yanagisawa, 1986)), while others establish temporary territories linked to the presence of 'shell nests' (e.g. *Lamprologus callipterus* (Schütz et al., 2016); *Telmatochromis vittatus* (Ota et al., 2012); no such 'shell nests' were present in our study plots). Finally, most Lake Tanganyika cichlids are territorial in reproductive



**FIGURE 2** Locations and general overview of the plots considered in this study. (a) shows a map of the study site in southern Lake Tanganyika (the whole lake seen in the insert), with Plots 1 and 2 located west of Mpulungu, Zambia and Plot 3 off of Mbita Island. Panels (b), (c) and (d) show images of the reconstructed habitats at Plot 1, 2, and 3, respectively (also referenced in panel (a))

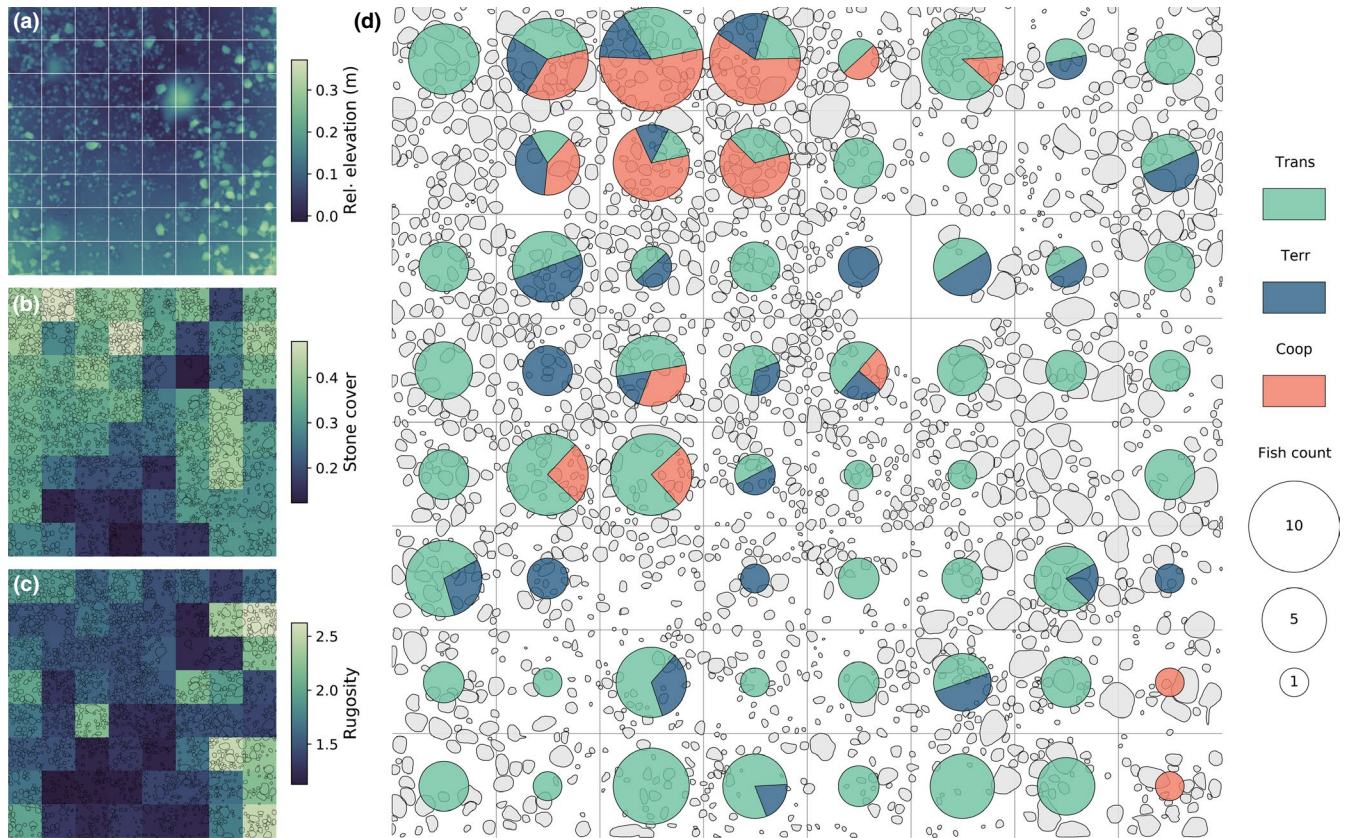
Classification	Species / Taxon
transient	<i>Altolamprologus compressiceps</i> (b), <i>Interochromis loockii</i> (f), <i>Lamprologus callipterus</i> (b), <i>Lepidiolamprologus attenuatus</i> (b), <i>Lepidiolamprologus elongatus</i> (b), <i>Lepidiolamprologus lemairii</i> (b), <i>Mastacembalus</i> spp. (p), <i>Neolamprologus modestus</i> (b), <i>Neolamprologus tetracanthus</i> (b), <i>Ophthalmotilapia ventralis</i> (f), <i>Perissodus</i> spp. (b), <i>Telmatochromis vittatus</i> (b, p), <i>Tropheus moorii</i> (f, p), <i>Xenotilapia</i> spp.
territorial	<i>Eretmodus cyanostictus</i> (f, p), <i>Telmatochromis temporalis</i> (b, p), <i>Variabilichromis moorii</i> (b, p)
cooperative	<i>Julidochromis ornatus</i> (b, p), <i>Neolamprologus pulcher</i> (b, p), <i>Neolamprologus savoryi</i> (b, p)

Note: Letters in brackets behind species names indicate whether rocks (or snail shells) serve the following roles for the respective species: (b) substrate for breeding, (f) substrate for primary food source [i.e., algae and invertebrates], (p) shelter for protection from predation (see Methods for details).

contexts, either defending a temporary breeding territory in which eggs and offspring are guarded (e.g., *Lepidiolamprologus attenuatus* and *Lepidiolamprologus elongatus* (Ochi & Yanagisawa, 1998); such territories can be maintained for several (serial) breeding attempts) or 'lekking' on such territories (e.g., *Ophthalmotilapia ventralis* (Haesler et al., 2009); no such breeding or lekking territories were present in our study plots). As such, the classifications of species as provided in this manuscript (Table 1) should be seen as adjusted for the aims and scopes of this current work, rather than as general biological observations. Our species list also notably omits various groups of Lake

Tanganyika fishes (including large cichlids (e.g., *Lobochilotes labiatus* or *Petrochromis* spp.), catfishes, sardines and Nile perches) because they are absent or very rare in these plots or because they are difficult to observe during direct visual surveys (Widmer et al., 2019). Each 1 × 1 m quadrat was observed for 1 min from approximately 1 m distance, requiring the entering of the plot for data collection at the inner quadrats. Hence, we elected to proceed in the following fashion: we first observed the south-eastern most quadrat and subsequently moved west. Once all eight southern-most quadrats had been sampled, we moved north and then east. We continued with

**TABLE 1** The classifications of the 20 focal species as used in this manuscript as either 'transient', that is not holding a permanent territory within the range of a 1 × 1 m quadrat, 'territorial', that is permanently defending a territory within the range of a quadrat, or 'cooperative', that is forming groups that permanently defend a territory within the range of a quadrat



**FIGURE 3** Various ways of data visualisation, using imaging and survey data for Plot 2. (a–c) give heat maps showing elevation (a), stone cover per quadrat (b) and rugosity per quadrat (c). (d) gives pie charts showing species category composition per quadrat. The size of each circle reflects the total number of individual fish observed, relative size of differently shaded areas gives composition (green: individuals of transient species; blue: individuals of territorial species; red: individuals of cooperative species; see Table 1). In (b–d) data are superimposed on a map showing outlines of stones

this 'snake-like' pattern, moving north and alternating between eastward and westward sampling of rows.

Filming commenced in a similar fashion to the surveys: swimming at a speed of ~15 m/min with the camera (GoPro Hero 5) held approximately 0.5 m above the ground, we covered each plot in a total of 9 videos. Starting at a haphazardly chosen corner, we swam along the outer edge of the plot (e.g., westward), centring the camera on the line delimiting the plot. Upon reaching the respective orthogonal border of the plot, we turned and swam back in the opposite direction (e.g., eastward), centring the camera on the middle of a given row of quadrats. We repeated this process of filming an outer edge and the centre of a row of quadrats a total of eight times, with the ninth video only capturing the line delimiting the plot on the side opposite to our starting point.

## 2.2 | Extraction of environmental data

We 3D-reconstructed each of the plots using the general-purpose Structure-from-Motion (SfM) and Multi-View Stereo (MVS) software COLMAP (v3.6) (Schönberger & Frahm, 2016), (Schönberger et al., 2016). SfM is a photogrammetric method aimed at estimating 3D information of a scene from a set of images (Hartley &

Zisserman, 2004), for example commonly used in archaeological 3D mapping (Willis et al., 2016). Here, we extracted still images from the recorded videos with a temporal sampling rate of 1 Hz (595, 595 and 643 images for Plot 1, 2 and 3, respectively). These images then served as input for the COLMAP SfM and MVS pipeline, which we followed through mainly with the software's default settings. We employed SfM to generate sparse 3D point clouds for the three plots and, additionally, the view-point position for each image. In a subsequent step, we used this information with MVS to reconstruct more detailed scenes by estimating depth maps for each image, which were then fused into coloured and dense 3D point clouds. This allowed for accurate reconstructions at a sub-centimetre resolution and approximately 30 million points per plot (37, 20 and 34 million points for Plot 1, 2 and 3, respectively; resolution of SfM reconstructions assessed and reviewed in, e.g., (Smith & Vericat, 2015)).

Next, we used MeshLab (v2020.07; (Cignoni et al., 2008)), an open-source software featuring 3D point cloud and mesh processing functions, to simplify the COLMAP output by resampling the point clouds to approximately one million points for each reconstruction. These simplified point clouds are still highly detailed but reduced the computational load for subsequent steps. Then, we used screened Poisson surface reconstruction (implemented in MeshLab; (Kazhdan & Hoppe, 2013)) to fit a mesh surface to the point cloud of each plot.

The 3D meshes were imported into Blender (v2.8; (Blender Online Community, 2020)) to generate high-resolution ( $3,840 \times 3,840$  pixels), orthographic renderings of each plot (see Figure 2), and for further processing to generate elevation maps. For the latter, we first scaled the reconstructions so that the corners of the nylon string grids were aligned with a horizontal,  $8 \times 8$  m plane in Blender coordinates. Then, we intersected a grid of equidistantly spaced, vertical planes (800 planes along both  $x$  and  $y$  axes, respectively) with the reconstructions. The resulting intersection points served as input to generate rasterized elevation maps ( $800 \times 800$  pixels, see Figure 3a) with a spatial resolution of 1 cm (using Python 3.8 and NumPy v1.19.0; (Harris et al., 2020)). Using these elevation maps, we computed the surface rugosity (i.e., surface area divided by projected area) of each  $1 \times 1$  m quadrat as a measure of environmental complexity.

Additionally, we segmented the reconstructions into stones (foreground) and sand (background) to calculate the relative stone cover as a proxy for the availability of defensible resources (Taborsky & Wong, 2017). Since an  $8 \times 8$  m plot can easily contain thousands of rocks (see Figure 3), we chose an automated approach that only requires minimal manual labelling of foreground objects. To this end, we trained an object detection and segmentation model (Mask R-CNN, open-source implementation in detectron2; (Wu et al., 2019)) on a limited set of 10 labelled images. These training images were cropped from the high-resolution Blender renderings and covered approximately 3% of the total reconstructed areas (2%, 6% and 2% of Plot 1, 2 and 3, respectively). The manual annotations were done using a Python-based GUI that was developed for animal tracking (Francisco et al., 2020), containing a total of 450 labelled foreground objects. We then trained a Mask R-CNN model on this small data set, using image augmentation techniques such as random rotations and resizing to avoid overfitting. After the training loss (i.e., the model's error on the training set) converged, we visually validated that the Mask R-CNN model was able to accurately segment foreground objects (stones) in the remaining plot areas (see Figure 3 for a complete segmentation of Plot 2). Ultimately, these segmentations were used to calculate stone cover as the ratio of the area covered by stones to the total area of each  $1 \times 1$  m quadrat.

## 2.3 | Statistical analysis

Using both species census data and the extracted environmental metrics, we tested whether fish abundance increased with higher stone cover or environmental complexity (rugosity). More specifically, we binned the observed species into three categories (transient, territorial, cooperative; see above and Table 1). To test potential effects of both environmental measures on per category fish counts, we fitted two negative binomial generalized linear models (nbGLMs). One model included fish count as response variable and including as predictors: stone cover, species category, plot ID and the second-order interactions between stone cover and species category, stone cover and plot ID and plot ID and species category.

An equivalent model was fitted for rugosity. When comparing these nbGLMs to similar models without the interaction terms with plot ID (using likelihood ratio tests on single term deletions), we found that most variation in the observed data was comprised in the differences between plots. Therefore, and based on the small number of plots, we chose to further analyse the relationships between habitat features and species distributions for each plot separately.

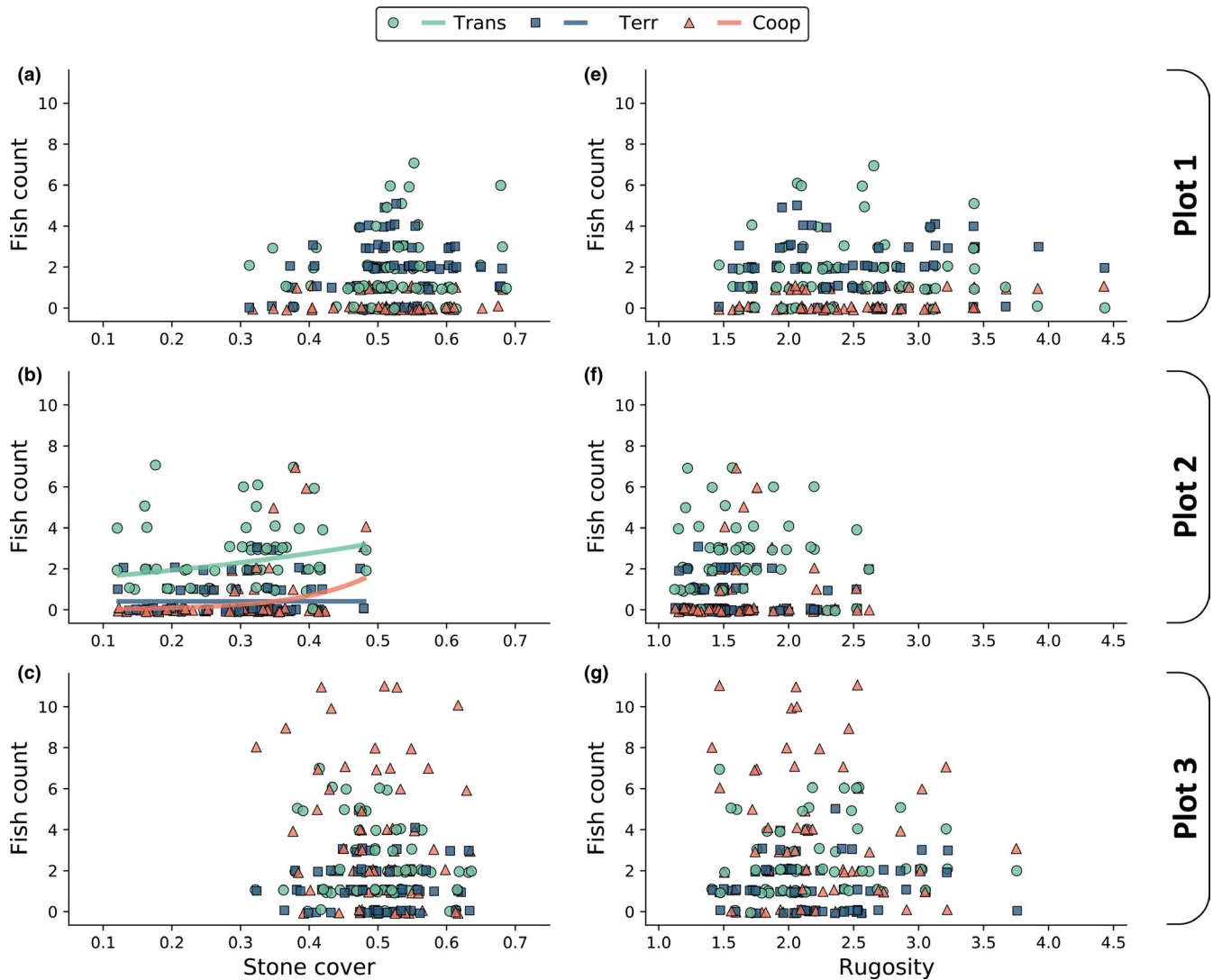
Following up on these initial models, a nbGLM was fitted for each of the two environmental measures (stone cover and rugosity) and for each plot, resulting in six models with fish count as response variable and the respective habitat feature (stone cover or rugosity), species category (transient, territorial, cooperative) and their second-order interaction as predictors. We then checked the models' residuals for spatial autocorrelation using Moran's  $I$  tests for each species category individually (for a total of 18 tests for spatial autocorrelation: one each per species category ( $n = 3$ ) per plot ( $n = 3$ ) per environmental measure ( $n = 2$ ); (Dormann et al., 2007), (Hartig, 2020)). If at least one of the three tests per plot indicated significant spatial autocorrelation of residuals, we included the locations of the species census observations (i.e., the coordinates of the  $1 \times 1$  m quadrats within the plot) as a spatially structured random effect, nested within species category (modelling a Gaussian decay of autocorrelation with distance between locations; (Dormann et al., 2007)). As before, we tested whether including the second-order interaction between the environmental measure and species category explained significantly more of the observed variance, and, if not, it was dropped from the models. Where interactions between species categories and stone cover or rugosity were found to significantly increase model fit, we tested for differences between species categories using Tukey post hoc tests in the 'multcomp' package (Hothorn et al., 2008). All models were fitted using the 'glmmTMB' package (v1.0.2.1; (Brooks et al., 2017)) and tested for goodness-of-fit with the 'DHARMA' package (v0.3.3.0; (Hartig, 2020)) in R (v4.0.2; (R Development Core Team, 2013)).

## 3 | RESULTS

### 3.1 | Stone cover

In Plot 1 (in front of Tanganyika Science Lodge at approximately 4 m depth), we detected no indication of spatial autocorrelation in the distributions of transient species (DHARMA Moran's  $I$  test (Moran's  $I$ ):  $SD = 0.015$ ,  $p = .25$ ), territorial species ( $SD = 0.015$ ,  $p = .27$ ) or cooperative species ( $SD = 0.015$ ,  $p = .89$ ), and thus did not include a spatially structured random effect in our models. Total fish numbers per quadrat were not influenced by a quadrat's stone cover (negative binomial generalised linear model (nbGLM): likelihood ratio test (LRT) = 2.1,  $p = .15$ ; Figure 4a) and there was no interactive effect between stone cover and species categories (LRT = 0.03,  $p = .99$ ).

In Plot 2 (in front of Tanganyika Science Lodge at approximately 11 m depth), we detected spatially autocorrelated distributions of cooperative species (Moran's  $I$ :  $SD = 0.014$ ,  $p < .001$ ), but not of



**FIGURE 4** The relationship between habitat features and counts of individual fish per quadrat. Panels (a–c) show data for stone cover, panels (e–g) for rugosity. Data are presented for both measures for all three plots: Plot 1: panels (a) and (e); Plot 2: panels (b) and (f); Plot 3: panels (c) and (g). In each panel, counts of individuals of transient species are in green (circles), those of territorial species in blue (squares), and those of cooperative species in red (triangles; see Table 1). Lines in (b) are coloured correspondingly and give the values predicted by the respective nbGLM (see Methods and Results) for the significant interactive effect of stone cover and species category on fish abundance in this plot. No other significant relationships were detected (see Results)

transient ( $SD = 0.016$ ,  $p = .78$ ) or territorial species ( $SD = 0.015$ ,  $p = .27$ ), and hence included a spatially structured random effect in our models. There was a significant interaction between stone cover and species category (nbGLM:  $LRT = 6.51$ ,  $p = .039$ ; Figure 4b), with stone cover being more strongly correlated with distributions of cooperative fish than with distributions of transient or territorial species (multiple comparisons of linear hypotheses: transient vs. territorial:  $z = 0.94$ ,  $p = .61$ ; transient vs. cooperative:  $z = 3.4$ ,  $p = .002$ ; territorial vs. cooperative:  $z = 2.65$ ,  $p = .02$ ).

In Plot 3 (at the south-western tip of Kumbula (Mbita) Island at approximately 7 m depth), we detected spatial autocorrelation in the distributions of transient (Moran's I:  $SD = 0.015$ ,  $p = .006$ ) and cooperative ( $SD = 0.015$ ,  $p < .001$ ) species, but not in the distributions of territorial species ( $SD = 0.015$ ,  $p = .93$ ). We consequently included a spatially structured random effect in our models. Total fish numbers

per quadrat were not influenced by a quadrat's stone cover (nbGLM:  $LRT = 1.14$ ,  $p = .29$ ; Figure 4c) and there was no interactive effect between stone cover and species categories ( $LRT = 3.04$ ,  $p = .27$ ).

### 3.2 | Rugosity

In Plot 1, we detected no indication of spatial autocorrelation in the distributions of transient species (Moran's I:  $SD = 0.015$ ,  $p = .39$ ), territorial species ( $SD = 0.015$ ,  $p = .1$ ) or cooperative species ( $SD = 0.015$ ,  $p = .71$ ), and thus did not include a spatially structured random effect in our models. Total fish numbers per quadrat were not influenced by a quadrat's stone cover (nbGLM:  $z = 0.59$ ,  $p = .56$ ; Figure 4e), and there was no interactive effect between stone cover and species categories ( $LRT = 1.36$ ,  $p = .51$ ).



In Plot 2, we detected spatially autocorrelated distributions of cooperative species (Moran's  $I$ :  $SD = 0.014$ ,  $p < .001$ ), but not of transient ( $SD = 0.016$ ,  $p = .6$ ) or territorial species ( $SD = 0.015$ ,  $p = .19$ ), and hence included a spatially structured random effect in our models. There was no interaction between rugosity and species category (nbGLM:  $LRT = 2.78$ ,  $p = .25$ ; Figure 4f), and rugosity did not correlate with total fish count in a given quadrat ( $z = 1.28$ ,  $p = .2$ ).

In Plot 3, we detected spatial autocorrelation in the distributions of transient (Moran's  $I$ :  $SD = 0.015$ ,  $p < .001$ ) and cooperative ( $SD = 0.015$ ,  $p < .001$ ) species, but not in the distributions of territorial species ( $SD = 0.015$ ,  $p = .94$ ). We consequently included a spatially structured random effect in our models. Total fish numbers per quadrat were not influenced by a quadrat's rugosity (nbGLM:  $z = 0.16$ ,  $p = .88$ ; Figure 4g) and there was no interactive effect between rugosity and species categories ( $LRT = 3.92$ ,  $p = .14$ ).

## 4 | DISCUSSION

Using a combination of visual census data and modern imaging and processing technology (Figure 1), we have shown here that information on habitat features and species distributions can be rapidly recorded for Lake Tanganyika cichlids. Our data reveal great variation in stone cover and rugosity within and between plots (Figure 2), with Plot 2 scoring particularly low in both these measures (Figure 3, Figure 4). Interestingly, it is precisely in this plot that we observe the anticipated correlation between the distribution of cooperatively breeding fish and increased availability of stones (Figure 3b). While transient and territorial (non-cooperative) fish did not show an association with habitat features in any of our plots, cooperative cichlids were also not more or less likely to be found in areas of increased rugosity or with higher stone cover when stones were generally abundant (i.e., in Plots 1 and 3; Figure 3a, Figure 3c). As such, we do find some support for the hypothesis that cooperative cichlids are more closely associated with the resource crucial for their survival and reproduction than non-cooperative fishes, but this being only truly observable where such substrate is scarce.

At least three factors may have contributed to the fact that the pattern we expected to find did not emerge in our data as clearly and generally as we had predicted. First, the plots were initially chosen based on requirements of a different study, thus not presenting a gradient of habitat features, but rather including two very rocky and one rather sandy plot (Figure 2). Second, the spatial resolution of the species survey data is probably too coarse to detect territorial and cooperative species mutually excluding each other—we often found many individuals of both categories in the same  $1 \text{ m}^2$  quadrat. In addition, a single survey may prove insufficient to capture the true composition of the local fish fauna (Widmer et al., 2019). Finally, the habitat features we investigated here, despite having been widely used in the past (Shumway et al., 2007), may be inadequate to truly detect 'resource quality', that is the actual number of shelters and realised protection they provide (Finstad et al., 2007). Our work here should thus be interpreted as an initial proof-of-concept

for the feasibility and usefulness of the techniques we applied. As such, future studies should aim to include a greater number of gradually differing plots, should collect species abundance data at smaller geographic scales (potentially also employing video-based surveying techniques to increase reliability of survey data (Widmer et al., 2019) and/or behavioural recordings (Francisco et al., 2020); this would also allow for re-analyses of species identities if observers were initially insufficiently trained to reliably identify fish down to the species level, the reason for our indiscriminate treatment of *Mastacembelus spp.*, *Perissodus spp.* and *Xenotilapia spp.*), should explore additional statistical approaches (e.g., nested models or Bayesian inference) and should identify those measures of habitat features that are most biologically relevant.

A key advantage of the procedures used here is their time efficiency in the field. Especially for SCUBA based work, using video-based approaches to record habitat information is beneficial: the two limiting factors for data collection during underwater fieldwork are the number of dives per field trip and the duration of each dive. With the latter restricting the amount of information that can be collected during a dive, time intensive works, for example the manual mapping of an area, eat into the budget of total dives available. Consequently, collating detailed maps used to require large investments of precious field time (e.g., (Heg et al., 2005), (Matsumoto & Kohda, 2007), (Sturmbauer, Fuchs, et al., 2008), (Tanaka et al., 2015), (Josi et al., 2020)). The work described here took a total of three dives per plot, one each for setting up the grid, conducting the survey and filming, respectively. Even the time requirements in the office are likely not much higher for our (largely automated) approach compared to classic, manual ways of mapping, the latter requiring the transcribing of underwater sketches into digital form for analysis and publication. As such, the sheer quantity of data that can be collected during a field expedition is much greater with these modern techniques.

In addition, the quality and resolution yielded by the filming and subsequent reconstruction of a given habitat offers various advantages. First, classic maps, especially those of underwater ranges, were typically two-dimensional with limited three-dimensional information at best (Heg et al., 2008), (Sturmbauer, Hahn, et al., 2008). By virtue of their three-dimensionality, reconstructed landscapes provide insights that were previously unobtainable (Ferrari et al., 2016). Second, by increasing the time spent filming and/or the number of recording devices, almost any level of resolution (in three dimensions) is possible (Woodget et al., 2015). Third, if combined with tracking techniques, the simultaneous collection of habitat and biological data is possible (Francisco et al., 2020). It is especially in this latter regard that modern imaging technology and subsequent analysis tools offer the greatest potential for the topic of this manuscript. The detailed recording of individual-level space use, inter-individual interactions and underlying habitat features will allow for much better observational and experimental inquiries into the interplay between defendable resources and the evolution of sociality and cooperation. For example, the excavation and maintenance of snail shells or shelters under rocks is a key behaviour that allows

lamprologine cichlids to gain maximum protection from their territories (Heg et al., 2004). However, this behaviour is energetically costly (Taborsky & Grantner, 1998) and thus constitutes an investment into a resource that is either monopolised by an individual or a group (Bergmüller et al., 2005), (Josi et al., 2020). This not only creates scope for synergistic effects of sociality, but also introduces conflicts of interest among group members (Rankin et al., 2007), (Strassmann & Queller, 2014). At the inter-specific level, sociality may indeed allow for the defence of high-quality habitat (as indicated by our data), but if resources become 'too attractive', this itself may bring in competition that cannot be overcome (Jordan et al., 2016). Future studies probing how individuals and groups alter their behaviour in response to changes in the quality of their defended resource and/or competition for it, applying the techniques outlined here and tracking individuals over extended periods of time (Jungwirth et al., 2019), will be insightful. Such longitudinal studies will also allow to estimate the degree to which animals actually alter the resources they defend, ideally investigating the degree to which sociality differs from solitary exploitation of a resource, either through the enlarged workforce of groups compared to loners or through the increased efficiency from division of labour (Rubenstein & Abbot, 2017).

An additional feature of Lake Tanganyika that is worth considering in this respect is the variability of habitats in which similar fish communities are found (Colombo et al., 2016). While traditionally three major classes of habitat have been described for Lake Tanganyika (Konings, 1998), namely (i) sandy, (ii) rocky and (iii) open water, more nuanced categories have been introduced over time (Clabaut et al., 2007). However, none of these categories truly reflect the continuous character of habitat differences. More objective and data-driven descriptions are thus desirable (Shumway et al., 2007). This is especially useful for comparisons between populations of the same species, where phenotypic traits, for example maximum size (Takahashi et al., 2009) or degree of sociality (Groenewoud et al., 2016), appear to correlate with habitat features. Such effects are already observable in the limited dataset we present here: while fish communities of all three plots overlapped considerably, habitat features differed greatly (Figure 2, Figure 4). What is more, intra-specific, inter-plot comparisons revealed differences in morphology, particularly maximum size (A. Jungwirth, unpublished data). As such, intra-specific and inter-population comparisons of habitat and phenotypes can give insight into the mechanisms of population divergence (Winkelman et al., 2014), which in turn may culminate in diversification and speciation as highlighted by other famous examples of adaptive radiations like those of Anoles lizards (Yuan et al., 2019). Obviously, the geographic and taxonomic scales that we consider here are much too small/narrow, for answering such questions, but the techniques we describe certainly offer the potential for collecting the necessary data at appropriate scales. Hence, detailed analyses of habitat, species distributions and individual behaviour as outlined in this manuscript not only lend themselves to studies of social evolution, but will also find use in ecological and evolutionary biology at large (Dell et al., 2014), (Hughey et al., 2018). Indeed,

this has already been demonstrated in a number of systems ranging from fish (Neuswanger et al., 2016), to birds (Groom et al., 2013), to mammals (Strandburg-Peshkin et al., 2017), to give just a very few examples of this rich literature. More generally, Structure-from-Motion and related image-based approaches, and environmental mapping techniques in general, have already revolutionised the fields of coral reef ecology (Fukunaga et al., 2019), cognitive ecology (Toledo et al., 2020) and collective behaviour (King et al., 2018), and we predict that behavioural and evolutionary scientists that have not yet included these means of data collection in their work will soon do so; the respective hardware and software become more and more accessible (Francisco et al., 2020) and any biological discipline interested in the mapping or quantifying of environmental features will greatly benefit from an increase in the quantity and quality of such data (King et al., 2018) including, but not limited to, conservation biologists interested in the effects of anthropogenic habitat alterations (Donohue et al., 2003) or the establishment of protected areas (Sweke et al., 2013).

Michael Taborsky's work over the past five decades has made important contributions to our understanding of social evolution, especially by dispelling misconceptions about the inability of fish to reach the levels of cooperative behaviour seen in other vertebrates (Taborsky & Limberger, 1981). A common theme throughout his work is the necessity for the existence of a sharable and defensible resource to enable stable and repeated interactions among individuals (Balshine et al., 2001), (Heg et al., 2008), (Taborsky, 2016), (Taborsky & Wong, 2017), opening the door for reciprocity and the collection and payment of 'rent' (Taborsky, 1985), (Heg et al., 2004), (van Doorn & Taborsky, 2012), (Zöttl et al., 2013), (Quiñones et al., 2016). With the advent of modern imaging and analytical technology, we can now tackle the question of whether defensible resources further contribute to the elaboration of cooperation and sociality, past its initial establishment. These are exciting times for anybody interested in social evolution and we hope Michael shares our enthusiasm.

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#### CONFLICT OF INTEREST

We declare that we have no conflicts of interest.

## ETHICAL APPROVAL

All applicable international, national and/or institutional guidelines for the care and use of animals were followed. The fieldwork reported here complied with Zambian laws and was carried out in agreement with local authorities under the Memorandum of Understanding issued by the Department of Fisheries: Ministry of Agriculture and Cooperatives, Zambia, dated 20th March 2009.

## DATA AVAILABILITY STATEMENT

All data and scripts will be made available by the authors upon reasonable request.

## ORCID

Arne Jungwirth  <https://orcid.org/0000-0002-2962-4015>

Paul Nührenberg  <https://orcid.org/0000-0001-6352-3560>

Alex Jordan  <https://orcid.org/0000-0001-6131-9734>

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