

## ORIGINAL PAPER

# Unprecedented Symbiont Eukaryote Diversity Is Governed by Internal Trophic Webs in a Wild Non-Human Primate



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Research on host-associated microbiomes has highlighted major divisions between the role of eukaryotes in free-living and symbiont systems. These trends call into question the relevance of macroecological processes to host-associated systems and the relative importance of parasitism, commensalism, and mutualism as evolutionary patterns across the domains of life. However, it is unclear as to whether these apparent differences reflect biological realities or methodologies in community characterization: free-living eukaryotes tend to be characterized using metabarcoding whereas symbiont eukaryotes are typically characterized with microscopy. Here, we utilize an Illumina high-throughput metabarcoding approach to characterize the diversity and dynamics of eukaryotic symbiont communities in the feces of a wild non-human primate, *Macaca fascicularis*, revealing functionally and taxonomically diverse communities of eukaryotes hitherto unreported from any vertebrate. Importantly, community assembly was consistent with top-down and bottom-up trophic food web dynamics, highlighting the applicability of macroecological principles to these communities. Ultimately, our findings highlight vertebrate-associated symbiont communities of the gut that are much more similar to free-living systems than previously realized. Additionally, our results support a role for symbiosis as a major recurrent life strategy among eukaryotes and highlight the potential for vertebrates to host vast reservoirs of unexplored eukaryotic diversity.

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## Introduction

The validity of any scientific principle is directly contingent on its general applicability. In this respect, the last decade of advances in microbiology might be said to have created a challenge for prevailing ecological and evolutionary theory. Microbial

prokaryotes have recently been suggested to account for an even larger proportion of the diversity of life on earth than previously anticipated (Locey and Lennon 2016), and vast amounts of prokaryotic diversity are now believed to occur as symbionts within the microbiome of multicellular eukaryotic life (Hug et al. 2016). In contrast, new discoveries in eukaryotic diversity have not kept up with these trends: eukaryotes appear to account for a drastically smaller fraction of life on earth

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than previously anticipated, and symbionts, which were historically believed to account for the majority of diversity within eukaryotes, now appear to account for only a miniscule fraction of this diversity (Costello 2016; Poulin 2014). While eukaryotes are still known to disproportionately act as dominant providers of vital ecosystem functions, such as primary production (Falkowski et al. 2004), decomposition (Dobrovolskaya et al. 2015), food web dynamics (Pernthaler 2005), carbon sequestration (Whitman et al. 1998) and niche construction (Cornwell et al. 2008) within most free-living communities and the biosphere at large, the new emphasis that microbiome studies have placed on symbiont communities and the links between these communities and the ecosystem at large have de-emphasized the relevance of eukaryotic functional ecology to many, and possibly most, communities, particularly if each free-living eukaryote may now be accepted to harbor its own community of principally prokaryotic symbionts. Taken together, these findings suggest a theoretical discrepancy between the eukaryotic vs prokaryotic, macroscopic vs microscopic, and symbiont vs free-living realms, and raise questions as to the capacity of existing ecological and evolutionary theory to provide universal explanations across the biosphere and the tree of life on earth.

The applicability of macroecological processes to microbial symbiont systems, nonetheless, remains a major outstanding question in unifying the field of community ecology (Sutherland et al. 2013). Eukaryotic symbionts may play an important role in bridging the gaps between macroscopic, microscopic, free-living, and host-associated communities, by virtue of their relatively untapped potential for demonstrating the universality of conserved keystone functional roles across all of these systems. Unfortunately, very little is currently known about the diversity and ecology of symbiont eukaryotes (Chabé et al. 2017; Hamad et al. 2016), and within vertebrates this deficit is particularly striking when compared with the vast amount of data that have been collected on symbiont prokaryotes (Clavel et al. 2016; Lloyd-Price et al. 2017; Sergeant et al. 2014; Thomas et al. 2016). While the ecology of vertebrate-associated eukaryotes has been hypothesized to resemble that of free-living eukaryotes, attempts to validate this hypothesis have met with ambiguous results. A handful of studies have suggested that vertebrate-associated eukaryotes are, like their free-living counterparts, regulated by predator-mediated top-down and resource-mediated bottom-up interactions (Graham 2008; Wilcox et al. 2015), but these

studies have relied on low-resolution microscopy based diagnostics, and lack a community ecology perspective. Eukaryotic microbiome studies, on the other hand, have found low richness community assemblages that exhibit inconsistent patterns of taxonomic association or distribution (Dollive et al. 2012; Foster et al. 2013; Gouba et al. 2014; Hamad et al. 2016; Parfrey et al. 2015). While these reports suggest minimal ecological or functional roles for eukaryotes within vertebrate hosts, they have generally relied on: older pyrosequencing approaches; low depths of read; relatively specific or untested amplicon primers that lacked direct comparability to free-living systems; small within-host sample sizes that may have failed to capture environmental variability in host habitat; and/or the use of either human or captive non-human hosts that may have demonstrated reduced eukaryotic diversity. Given the disproportionate and vital roles of eukaryotes in free-living systems, including as top microbial predators (Pernthaler 2005) and keystone decomposers (Dobrovolskaya et al. 2015), newer high-throughput approaches may elucidate vertebrate-associated eukaryotes as far more diverse, dynamic, and ecologically relevant than currently realized (Heitlinger et al. 2017).

Here, we use an Illumina HiSeq-based metabarcoding approach to characterize the eukaryotic communities of wild long-tailed macaques (*Macaca fascicularis*) from the islands of Singapore and Bali, Indonesia. We utilize two degenerate primer-pairs, adapted from studies on marine eukaryotes (Amaral-Zettler et al. 2009) to allow for assessment of the diversity captured by single primer-pairs and to facilitate comparisons with free-living biomes. We anticipate that our approach will reveal diverse and dynamic resident eukaryotic communities characterized by: 1) universally occurring symbiont groupings, taxonomic or trophic, suggestive of consistent roles for eukaryotes within *M. fascicularis*; 2) ecological responsiveness, suggesting interactions between resident eukaryotes and the broader environmental conditions of their *M. fascicularis* hosts; 3) patterns of co-assembly between functional groupings of eukaryotes in accordance with top-down and bottom-up trophic interactions, such that protozoa living off free nutrients (referred to here as “grazers”) will correlate to diet, predatory protozoa, which consume other organisms in the gut, will correlate to grazers and diet (due to their typical capacity to use free-nutrients as well), and that intracellular protozoa, which live off host nutrients rather than nutrient inputs, will not correlate to diet or grazers. We find levels of symbiont eukaryotic diversity that exceed those previously reported

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