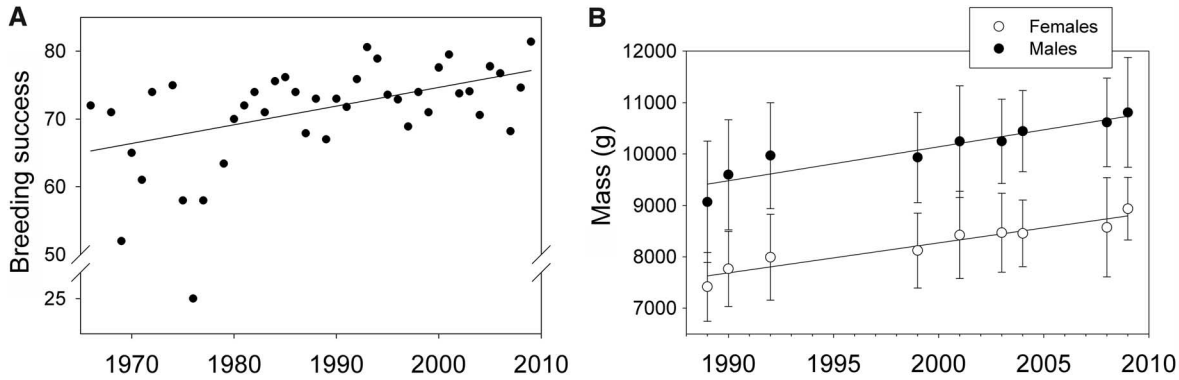

Fig. 4. (**A**) Changes in breeding success over the past 40 years ($r^2 = 0.30$, $P = 0.0003$). From 1988 to 2009 only, $r^2 = 0.19$, $P = 0.048$. (**B**) Changes over the past 20 years in the mass of breeding wandering albatrosses in January to February.

wandering albatrosses, the movements of many other species of albatrosses and petrels are strongly constrained by wind conditions (*8*, *21*), and species richness of Procellariiformes is positively associated to wind speed (*22*). Thus, future research should consider wind fields as an important driver of the distribution and migration of these oceanic species.

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Plant Species Richness and Ecosystem Multifunctionality in Global Drylands

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Experiments suggest that biodiversity enhances the ability of ecosystems to maintain multiple functions, such as carbon storage, productivity, and the buildup of nutrient pools (multifunctionality). However, the relationship between biodiversity and multifunctionality has never been assessed globally in natural ecosystems. We report here on a global empirical study relating plant species richness and abiotic factors to multifunctionality in drylands, which collectively cover 41% of Earth's land surface and support over 38% of the human population. Multifunctionality was positively and significantly related to species richness. The best-fitting models accounted for over 55% of the variation in multifunctionality and always included species richness as a predictor variable. Our results suggest that the preservation of plant biodiversity is crucial to buffer negative effects of climate change and desertification in drylands.

Two decades of research have revealed causal linkages between biodiversity and univariate measures of ecosystem functioning, such as primary productivity or nitrogen accumulation, in many terrestrial and aquatic habitats (*1*–*4*). These relationships suggest that the loss of biodiversity may impair the functioning of natural ecosystems and thus diminish

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the number and quality of services they provide (*5–7*). Ecosystems are valued for their ability to maintain multiple functions and services simultaneously [multifunctionality (*8*)]. If the maintenance of biodiversity is to be justified as a strategy for enhancing ecosystem services (*5, 9*), it is essential to understand how biodiversity affects multifunctionality (*8–10*). Existing knowledge comes from controlled small-scale experiments from a limited number of ecosystems, mainly in North America and Europe (*8–12*). Furthermore, biodiversity is by no means the only, or even the primary, driver of ecosystem functioning, which is also influenced by other biotic and abiotic factors (*13, 14*). Given this complexity, a rigorous examination is needed of the role of biodiversity in maintaining multifunctionality at a large number of sites that represent a wide range of spatial variability in resource availability, abiotic factors, and species richness and composition (*15*).

Arid, semi-arid, and dry-subhumid ecosystems (called hereafter "drylands") constitute some of the largest terrestrial biomes, collectively covering 41% of Earth's land surface and supporting over 38% of the global human population (*16*). Drylands host many endemic plant and animal species (*5*) and include about 20% of the major centers of global plant diversity and over 30% of the designated endemic bird areas (*17*). These ecosystems are also highly vulnerable to global environmental change and desertification (*16, 18*). Nevertheless, the relationship between biodiversity and ecosystem functioning has seldom been studied in drylands (*19*). We evaluated how the richness of perennial vascular plants (hereafter "species richness") and a range of key abiotic factors (climate, slope, elevation, and soil texture) relate to multifunctionality in 224 dryland ecosystems sampled from all continents except Antarctica (map S1). We surveyed plots measuring 30 m × 30 m, which were large enough to represent the main ecosystem features at each site, and assessed 14 ecosystem functions related to the cycling and storage of carbon (C: organic C, β-glucosidase, pentoses, hexoses, aromatic compounds, and phenols), nitrogen (N: total N, NO_3^--N, NH_4^+-N, aminoacids, proteins, and potential N transformation rate), and phosphorus (P: available inorganic P and phosphatase). These functions were chosen because they deliver some of the fundamental supporting and regulating ecosystem services (*9, 18, 20*) and because they are used to identify the onset of desertification processes (*21*). Our survey captured a substantial range of the climatic conditions, ecosystem types, and soil classes found in drylands worldwide (fig. S1 and map S1).

We first evaluated the direct relationship between species richness and multifunctionality at the global scale using both nonspatial [ordinary least-squares (OLS)] and spatial [simultaneous autoregression (SAR)] regression models (*20*). Because we did not experimentally control for other abiotic and biotic factors that are known to affect ecosystem functioning, significant relationships would indicate potentially strong effects of richness on multifunctionality. To quantify multifunctionality, we calculated *Z*-scores (standardized deviates) of the 14 functions evaluated (*20*). The multifunctionality index *M* for each plot was the average *Z*-score for all functions measured within the plot. This index measures all functions on a common scale of standard deviation units, has good statistical properties, and is well correlated with previously proposed indices for quantifying multifunctionality (*20*) (fig. S4). Multifunctionality was positively and significantly ($P < 0.05$) related to species richness, according to both OLS and SAR models (Fig. 1A). Separate analyses of functions related to the C, N, and P cycles (*20*) also yielded positive and significant relationships with species richness in all cases when using OLS regression (Fig. 1, B to D). When SAR regressions were used, significant relationships were found only for functions related to C cycling (Fig. 1, B to D).

We then evaluated whether the observed effects of species richness were important as compared to those of abiotic factors, with a multimodel inference approach based on information theory and OLS regression (*22*). We built separate models using the multifunctionality index *M* and functions from the N, C, and P cycles as dependent variables, and seven abiotic variables [sand content, slope, elevation, and four components derived from a principal-components analysis of 21 available climatic variables (*20*)] plus species richness as potential independent variables. Among the 255 possible models resulting from all possible combinations of these independent variables, we selected the set of best-fitting models that minimized the second-order Akaike information criterion (AIC_c). Collinearity among independent variables in these models was negligible (*20*) (table S15). Whenever a model included species richness as an important predictor, we compared its AIC_c to that of the corresponding model without species richness; differences < 2.0 in AIC_c between alternative models indicate that they are approximately equivalent in explanatory power (*22*). To account for potential effects of spatial autocorrelation between sites, latitude and longitude were included in all the models (*23*).

The best and most parsimonious models (smallest AIC_c and fewest variables with comparable AIC_c, respectively) describing global multifunctionality contained 9 and 7 predictor variables (Table 1). Both models explained more than 55% of the variance found in multifunctionality, and included species richness. In both cases, the removal of species richness as a predictor variable substantially reduced the model fit (Table 1). These results were virtually identical to those obtained with SAR regression and OLS models that included quadratic terms, to account for potential autocorrelation and nonlinear effects, respectively (*20*) (tables S2 and S3), and for models that used other multifunctionality indices proposed in the literature (*20*) (table S13). Species richness

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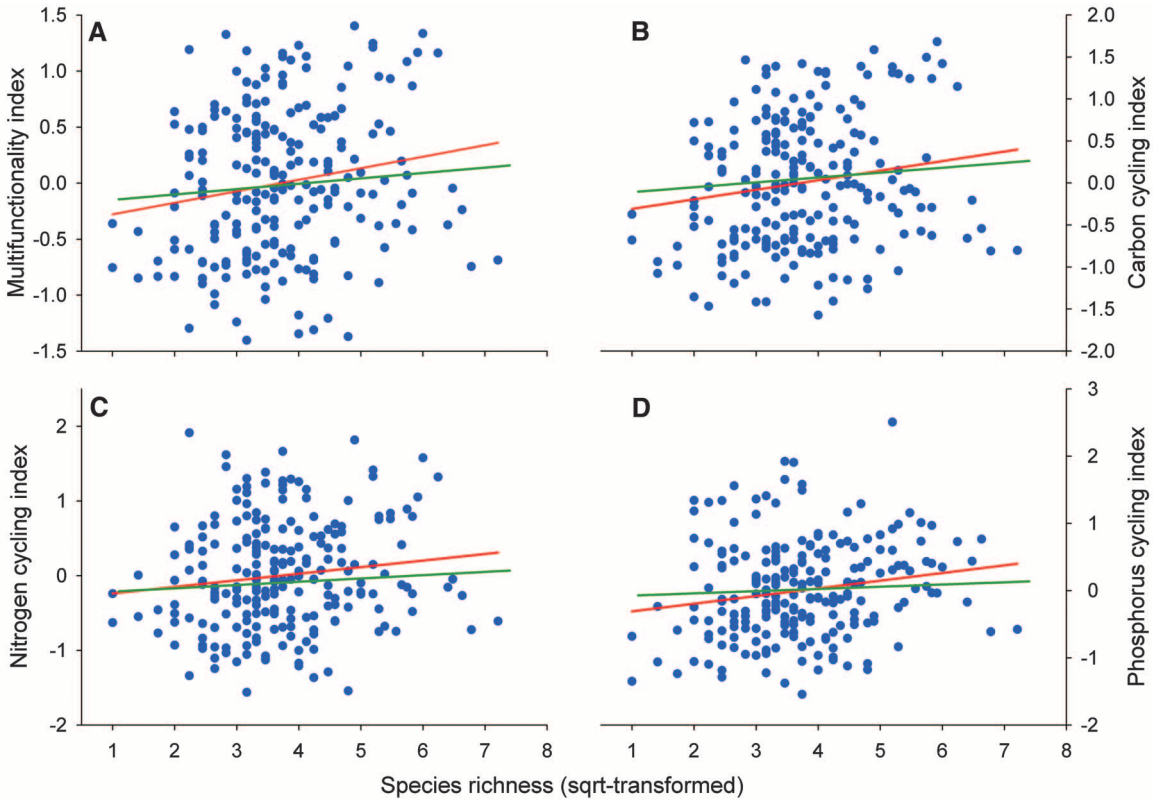

Fig. 1. Relationship between perennial plant species richness and ecosystem multifunctionality (**A**) measured in a global survey of drylands. Similar relationships for C (**B**), N (**C**), and P (**D**) cycling are shown. Red and green lines are the fitted lines from OLS and SAR regressions, respectively. Results of regressions are as follows: (A) OLS, R^2 (percent of variation in multifunctionality explained by the model) = 0.030, P = 0.009; SAR, R^2 = 0.022, P = 0.027; (B) OLS, R^2 = 0.029, P = 0.011; SAR, R^2 = 0.022, P = 0.027; (C) OLS, R^2 = 0.018, P = 0.044; SAR, R^2 = 0.014, P = 0.082; and (D) OLS, R^2 = 0.032, P = 0.008; SAR, R^2 = 0.016, P = 0.061.

was also an important factor in separate models of C and N cycling (tables S4, S5, S7, S8, S10, and S11) but had weaker effects on P cycling (tables S6, S9, and S12). Overall, the general result that species richness makes important contributions to multifunctionality was robust to the analytical methods used and to the choice of multifunctionality index.

To quantify the relative importance of the different predictors of multifunctionality, we summed the Akaike weights for each predictor across all the models in which it occurred (*20, 22*); the larger this sum, the more important a given variable is relative to the other variables used in the same models. By this criterion, the two most important predictors of multifunctionality were annual mean temperature [reflected in large negative loadings for the fourth principal component of the climatic variables (*20*)] and the sand content of the soil (Fig. 2A). Both variables were negatively related to multifunctionality: Higher ecosystem functionality was found at cooler temperatures and lower sand content (table S14). The importance of species richness was very similar to that of mean temperature and sand content. Indeed, species richness was more important than climatic variables such as mean annual rainfall and mean temperature and rainfall in the driest quarter [reflected in loadings on the first and third principal components of the climatic variables, respectively (*20*)]. Similar results were obtained when functions related to the C and N cycles were evaluated separately (Fig. 2, B and C). Species richness was less important to P cycling than were other abiotic factors such as sand content, elevation, and annual rainfall (Fig. 2D).

Table 1. Best-fitting regression models of ecosystem multifunctionality. Each column represents a different predictor variable (red, perennial plant species richness; green, abiotic variables; blue, climatic variables; gold, geographic variables). Of all 255 possible models, the best 8 models are presented, ranked according to AIC_c value. AIC_c measures the relative goodness of fit of a given model; the lower its value, the more likely it is that this model is correct. Unshaded cells indicate variables that were not included in a particular model. The first and third models of the table are the best and most parsimonious models, respectively; the same models without species richness had R^2 = 0.539, AIC_c = 293.236, ΔAIC_c = 10.486; and R^2 = 0.515, AIC_c = 300.078, ΔAIC_c = 17.328, respectively. ΔAIC_c, difference between the AIC_c of each model and that of the best model; w_i, Akaike weights; C1, C2, C3, and C4, first, second, third, and fourth components of a principal-components analysis conducted with climatic variables; SA, sand content; SL, slope angle (square root–transformed); EL, elevation (square root–transformed); LA, latitude; and LO, longitude.

Species richness	Abiotic		Climatic				Geographic			R^2	AIC_c	ΔAIC_c	w_i
	SL	SA	C1	C2	C3	C4	LA	LO	EL				
										0.564	282.750	0	0.217
										0.559	283.226	0.475	0.171
										0.554	283.595	0.845	0.143
										0.558	283.862	1.111	0.125
										0.565	284.502	1.751	0.091
										0.556	284.637	1.887	0.085
										0.561	284.677	1.927	0.083
										0.560	285.035	2.285	0.069

The positive effects of species richness on multifunctionality may be mediated through increased net primary production (NPP), which has cascading effects on multiple organisms and ecosystem processes (*1, 24*). However, the relationship between plant species richness and NPP is uncertain (*25*), and NPP could not be measured in this study. We speculate instead that complementarity in the use of resources such as water (*2, 9*), which has been demonstrated in drylands and can occur without changes in NPP (*26, 27*), accounts for correlations between species richness and multifunctionality. Our results also implicate soil water conditions, which are largely affected by temperature and soil texture (*28*), as an important driver of multifunctionality.

By itself, species richness accounted for only a small fraction of the observed variation in the

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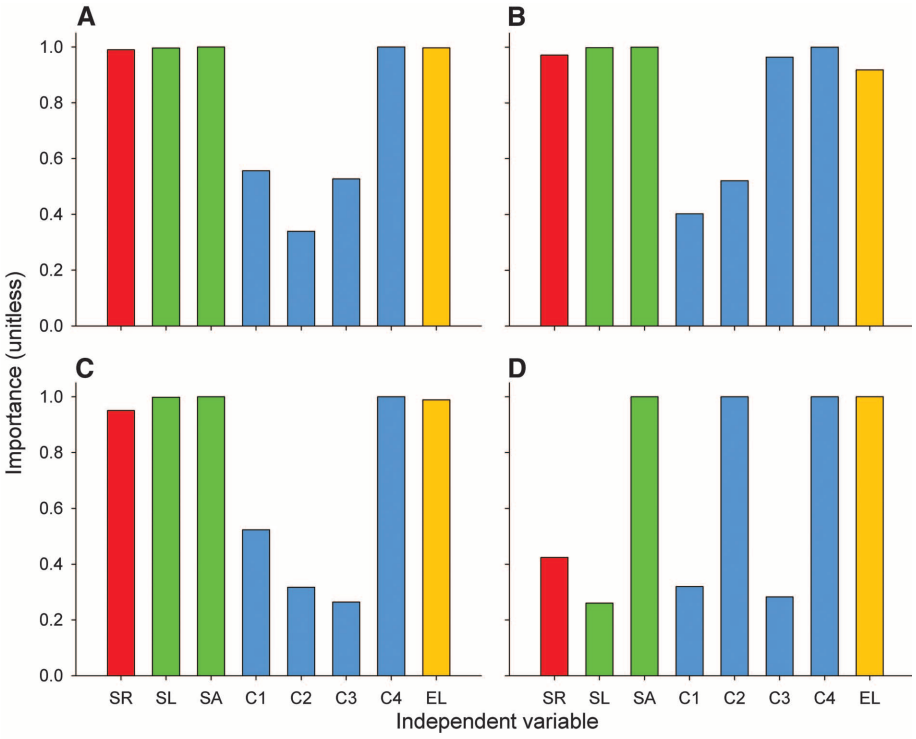

Fig. 2. Relative importance of perennial plant species richness (red column) and other predictor variables in models of ecosystem multifunctionality (**A**) and C (**B**), N (**C**), and P (**D**) cycling. The height of each bar is the sum of the Akaike weights of all models that included the predictor of interest, taking into account the number of models in which each predictor appears. Variable abbreviations are as in Table 1.

multifunctionality of drylands (Fig. 1). However, the best-fitting models accounted for over 55% of this variation and always included species richness (Table 1). The unexplained variation probably reflects factors not measured in our global survey, including the intensity of herbivory, historical patterns of land use, the presence of keystone and invasive species, and differences in components of biodiversity such as soil fauna, whose changes along environmental gradients do not necessarily track those of plant richness (*28–30*).

Climate change models predict increases in average annual temperature in drylands of up to 4°C by the end of the 21st century (*31*). Our results suggest that such an increase will reduce the ability of dryland ecosystems to perform multiple functions related to C, N, and P cycling. Ongoing climate change is also likely to reduce local species richness (*32*) and to increase the extent of areas affected by desertification (*16, 18*), both of which will negatively affect ecosystem functioning. However, these outcomes are uncertain because of the complex interactions and contrasting effects of increases in temperature, which we found to reduce multifunctionality, and in atmospheric carbon dioxide concentrations, which can ameliorate water stress in dryland vegetation and potentially minimize biodiversity losses (*33, 34*). Because the quality and quantity of ecosystem services depend largely on ecosystem functions such as those measured in this study (*5, 9*), increased plant species richness may enhance the services provided by dryland ecosystems. Our findings also suggest that such richness may be particularly important for maintaining ecosystem functions linked to C and N cycling, which sustain C sequestration and soil fertility (*18, 28*). Because land degradation is often accompanied by the loss of soil fertility (*16, 18*), plant species richness may also promote ecosystem resistance to desertification.

The consistent effects of species richness on multifunctionality over and above those of climate and of abiotic factors highlight the importance of plant biodiversity as a driver of multifunctionality in drylands. The positive relationship between species richness and multifunctionality found is consistent with experimental results obtained in temperate grasslands and in microbial, biological soil crust, and aquatic communities (*8–12*). Collectively, these results suggest that the correlation between species richness and multifunctionality may be a general pattern in nature that reflects a cause-and-effect linkage.

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F.T.M. and A.E. designed the study. Field data were collected by all authors except A.E., A.G., N.J.G., B.G., E.V., and M.B. Laboratory analyses were done by V.O., A.G., M.B., M.D.B., E.V., and B.G. Data analyses were done by F.T.M., assisted by N.J.G. The paper was written by F.T.M., and all authors contributed to the subsequent drafts.

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A DOC2 Protein Identified by Mutational Profiling Is Essential for Apicomplexan Parasite Exocytosis

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Exocytosis is essential to the lytic cycle of apicomplexan parasites and required for the pathogenesis of toxoplasmosis and malaria. DOC2 proteins recruit the membrane fusion machinery required for exocytosis in a Ca^{2+}-dependent fashion. Here, the phenotype of a *Toxoplasma gondii* conditional mutant impaired in host cell invasion and egress was pinpointed to a defect in secretion of the micronemes, an apicomplexan-specific organelle that contains adhesion proteins. Whole-genome sequencing identified the etiological point mutation in TgDOC2.1. A conditional allele of the orthologous gene engineered into *Plasmodium falciparum* was also defective in microneme secretion. However, the major effect was on invasion, suggesting that microneme secretion is dispensable for *Plasmodium* egress.

The lytic replication cycle is central to the pathology of apicomplexan diseases such as malaria caused by *Plasmodium* spp. and toxoplasmosis caused by *Toxoplasma gondii*. Motility of parasites between host cells, within which replication occurs, is powered by actinomyosin motors connecting with extracellular substrate through transmembrane adhesion proteins secreted through organelles known as micronemes (*1*). A pivotal event in triggering motility is the release of Ca^{2+} from compartments within the parasite, which activates myosin and triggers microneme secretion (*2*). Recently, calcium-dependent protein kinases required for egress were identified in *Plasmodium falciparum* (PfCDPK5) and *Toxoplasma* (TgCDPK1) (*3*, *4*).

To investigate this critical process, we used temperature-sensitive mutants in the lytic cycle of *Toxoplasma* by means of chemical mutagenesis (*5*). Upon phenotype induction, mutant F-P2 displayed a reduced invasion competency (Fig. 1A) and complete inability to egress (*6*), but intracellular growth progressed normally (*6*). Three distinct Ca^{2+}-dependent events are required for egress and invasion: extrusion of the apical conoid, motility, and microneme secretion. Conoid extrusion in F-P2 was indistinguishable from wild-type parasites (Fig. 1B and figs. S1 and S5C) (*7*–*9*). Motility was assessed via video microscopy, and the incidence of the three motility modes of *Toxoplasma* tachyzoites (circular and helical gliding and twirling) (movies S1 to S3) were scored (*9*, *10*). Under

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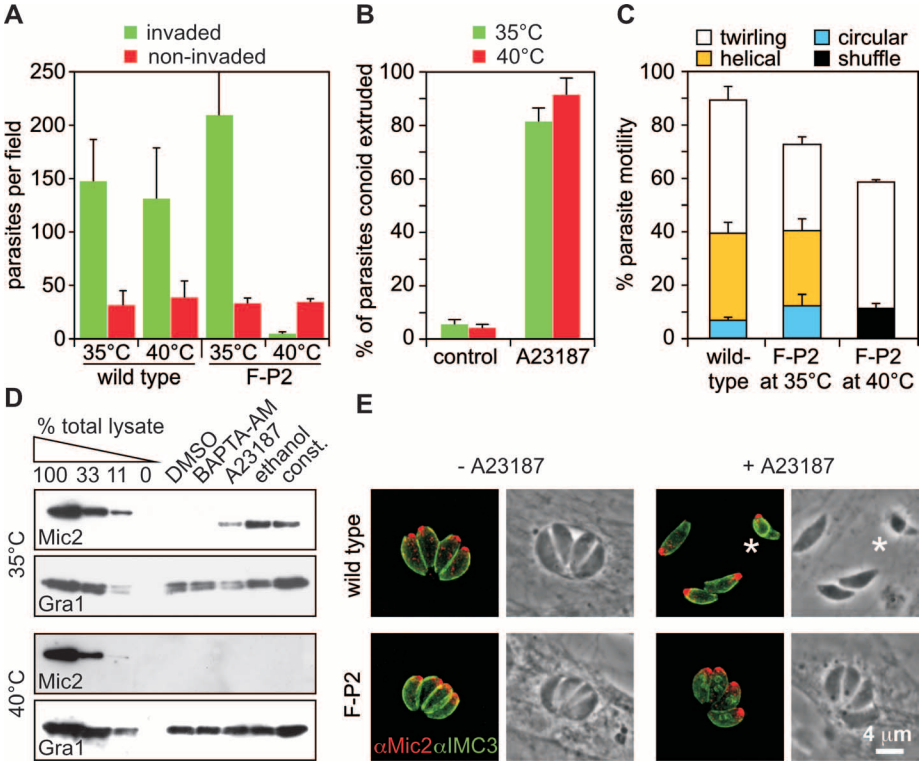

Fig. 1. Mutant F-P2 has a microneme secretion defect. (**A**) Red-green invasion assays were performed on the 2F-1-YFP2 wild-type and F-P2 mutant parasite lines. Parasites were phenotypically induced for 24 hours at the restrictive temperature (40°C). Averages of four independent experiments +SD are shown. (**B**) Conoid extrusion of Ca^{2+}-ionophore (A23187)–induced or vehicle control–treated parasites was determined for parasites grown at 35° or 40°C. Averages of three independent experiments +SD are shown. (**C**) Incidence of various motility modes determined by video microscopy over 1 min for wild-type (parent 2F-1-YFP2) and F-P2 parasites at conditions as indicated. Averages of four independent experiments +SEM are shown. (**D**) Microneme secretion of F-P2 parasites measured by means of Western blot detection of Mic2 protein released in the supernatant upon various stimuli and vehicle control (dimethyl sulfoxide). "const." represents uninduced, constitutive secretion over a 60-min period. Gra1 serves as loading control. (**E**) Immunofluorescence assay of Mic2 and IMC3 (marking the peripheral cytoskeleton) of wild-type and F-P2 at 40°C with or without ionophore stimulation shows micronemes are intact in F-P2. Phase images show vacuolar membrane is intact in F-P2 at 40°C. Asterisks mark the egressing parasite.

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