

Large-scale coral reef restoration could assist natural recovery in Seychelles, Indian Ocean

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Abstract

The aim of ecological restoration is to establish self-sustaining and resilient systems. In coral reef restoration, transplantation of nursery-grown corals is seen as a potential method to mitigate reef degradation and enhance recovery. The transplanted reef should be capable of recruiting new juvenile corals to ensure long-term resilience. Here, we quantified how coral transplantation influenced natural coral recruitment at a large-scale coral reef restoration site in Seychelles, Indian Ocean. Between November 2011 and June 2014 a total of 24,431 nursery-grown coral colonies from 10 different coral species were transplanted in 5,225 m² (0.52 ha) of degraded reef at the no-take marine reserve of Cousin Island Special Reserve in an attempt to assist in natural reef recovery. We present the results of research and monitoring conducted before and after coral transplantation to evaluate the positive effect that the project had on coral recruitment and reef recovery at the restored site. We quantified the density of coral recruits (spat <1 cm) and juveniles (colonies 1–5 cm) at the transplanted site, a degraded control site and a healthy control site at the marine reserve. We used ceramic tiles to estimate coral settlement and visual surveys with 1 m² quadrats to estimate coral recruitment. Six months after tile deployment, total spat density at the transplanted site (123.4 ± 13.3 spat m⁻²) was 1.8 times higher than at healthy site (68.4 ± 7.8 spat m⁻²) and 1.6 times higher than at degraded site (78.2 ± 7.17 spat m⁻²). Two years after first transplantation, the total recruit density was highest at healthy site (4.8 ± 0.4 recruits m⁻²), intermediate at transplanted site (2.7 ± 0.4 recruits m⁻²), and lowest at degraded site (1.7 ± 0.3 recruits m⁻²). The results suggest that large-scale coral restoration may

have a positive influence on coral recruitment and juveniles. The effect of key project techniques on the results are discussed. This study supports the application of large-scale, science-based coral reef restoration projects with at least a 3-year time scale to assist the recovery of damaged reefs.

Keywords

Reef recovery, coral transplantation, coral settlement, coral recruitment, Acroporidae, Pocilloporidae, Western Indian Ocean

Introduction

A key principle in ecological restoration is to re-establish self-sustaining and resilient ecosystems, similar to their reference ecosystems (Shackelford et al. 2013; Suding et al. 2015). Due to the continued decline of coral reefs worldwide (Hughes 2003; Pratchett et al. 2014), restoration of damaged coral reefs has been recommended as a strategy to assist in reef recovery (Rinkevich 1995, 2008). Restoration of damaged reefs by transplantation of nursery-grown coral colonies increases coral cover, species diversity, coral reproduction capacity and local recruitment (Richmond and Hunter 1990; Horoszowski-Fridman et al. 2011). If donor coral colonies are the survivors of previous bleaching events, coral transplantation increases the spread of bleaching-resistant genotypes and improves resilience (Edwards 2010; Mascarelli 2014). In coral reef restoration, long-term sustainability relies on enhancement of coral recruitment: transplants become an additional source of recruits, or recruits from elsewhere are attracted to the transplanted site by settlement cues associated with the presence of new corals (Kingsford et al. 2002; Sponaugle et al. 2002; Gleason et al. 2009; Dixson et al. 2014).

The 1998 mass coral bleaching event severely affected the reefs of the Indian Ocean (Spencer et al. 2000; Spalding and Jarvis 2002) with 30% mortality recorded at a regional level (Obura 2005). In the Seychelles Archipelago alone, live coral cover decreased to less than 3% in some areas (Graham et al. 2006). Since 1998, recovery has been extremely slow in the inner granitic islands of Seychelles (Graham et al. 2006; Chong-Seng et al. 2014; Harris et al. 2014). Such slow post-bleaching recovery motivated active restoration efforts in the inner Seychelles to assist natural recovery (Frias-Torres et al. 2014). Between November 2011 and June 2014 a total of 24,431 nursery-grown coral colonies from 10 different branching and tabular coral species were transplanted in 5,225 m² (0.52 ha) of degraded reef at the no-take marine reserve of Cousin Island Special Reserve (Frias-Torres et al. 2014; Frias-Torres and van de Geer 2015; Frias-Torres et al. 2015).

Could coral transplantation have a positive effect on coral recruitment and therefore enhance reef recovery at the restored site? Coral recruitment did not change when comparing sites with coral settlement structures with and without coral transplants (Maldives, Clark and Edwards 1995) or comparing with untouched control areas (Indonesia, Ferse et al. 2013). Both studies recommended coral transplantation as a last resort when reef recovery is hindered due to limited natural recruitment. When coral fragments were transplanted directly to the natural reef substrate, coral recruitment in transplanted areas

was higher than in denuded non-transplanted areas (Tanzania, Mbiye et al. 2013). From these studies it is unclear whether coral transplantation is effective in enhancing natural coral recruitment or in accelerating reef recovery. Such uncertainty hinders the cost-effectiveness of ongoing and future coral transplantation projects. A possible limitation in our understanding of the effectiveness of coral transplantation is due to the small scale of transplant studies (<0.1 ha) compared to the scale of reef damage, because the transplantation of nursery-reared colonies to a degraded reef at small scales might be insufficient to enhance local coral recruitment (Edwards and Gomez 2007).

Our aim was to evaluate the effects of large-scale coral restoration on coral recruitment in a no-take marine reserve. We assessed the spatial differences in natural coral recruitment and juveniles after coral transplantation. We quantified coral recruitment and juveniles at the transplanted site and two untouched sites: healthy and degraded. The healthy and degraded sites served as a reference for natural coral recruitment. We hypothesized that coral recruitment and juveniles would be highest at the healthy site, intermediate at the transplanted site, and lowest at the degraded site. This study will contribute to our understanding of the effectiveness of large-scale coral restoration in enhancing natural coral recruitment or in accelerating reef recovery.

Methods

Study site

The study site was a continuous fringing reef on the south-west side of Cousin Island (Figure 1). The reef is approximately 400 m long and 30 m wide (ca. 1.2 ha), ranging in depth between 6.5 and 13 m. Corals of a 40 m long section of the reef at its southernmost end (4°20'09"S, 55°39'32"E) survived the 1998 mass coral bleaching event. This survivor section became the healthy site (ca. 0.12 ha), one of the untouched reference sites. Coral cover in this section of the reef has shown good recovery from <15% in 2012 to <35% in 2014 (Figure 1), and is dominated by *Acropora* (e.g. *A. appressa*, *A. cytherea*, *A. humilis*, *A. hyacinthus*) and *Pocillopora* (*P. grandis* and *P. verrucosa*) species. Coral cover in the remainder of the reef (ca. 1 ha) was less than 3%. Here, a 50-m long section of the reef, north-west (4°20'08"S, 55°39'30"E) of the healthy site, was selected as the degraded site (ca. 0.13 ha), the other untouched reference site, where a mix of consolidated, unconsolidated rubble and sand dominate the substrate, and coral cover has remained unchanged since 2012 (Figure 1). A 150-m long section of the degraded reef north (4°20'04"S, 55°39'25"E) of the degraded site was targeted for restoration through coral transplantation. This was the transplanted site (0.52 ha), where the substrate resembled the degraded site in 2012. Although 10 different branching/tabular species were transplanted in this site (*Acropora cytherea*, *A. damicornis*, *A. formosa*, *A. hyacinthus*, *A. abrotanoides*, *A. lamarki*, *A. vermiculata*, *Pocillopora damicornis*, *P. indiania*, *P. grandis* and *P. verrucosa*; species identification after Veron 2000 and nomenclature after the World Register of Marine Species [www.marinespecies.org]),

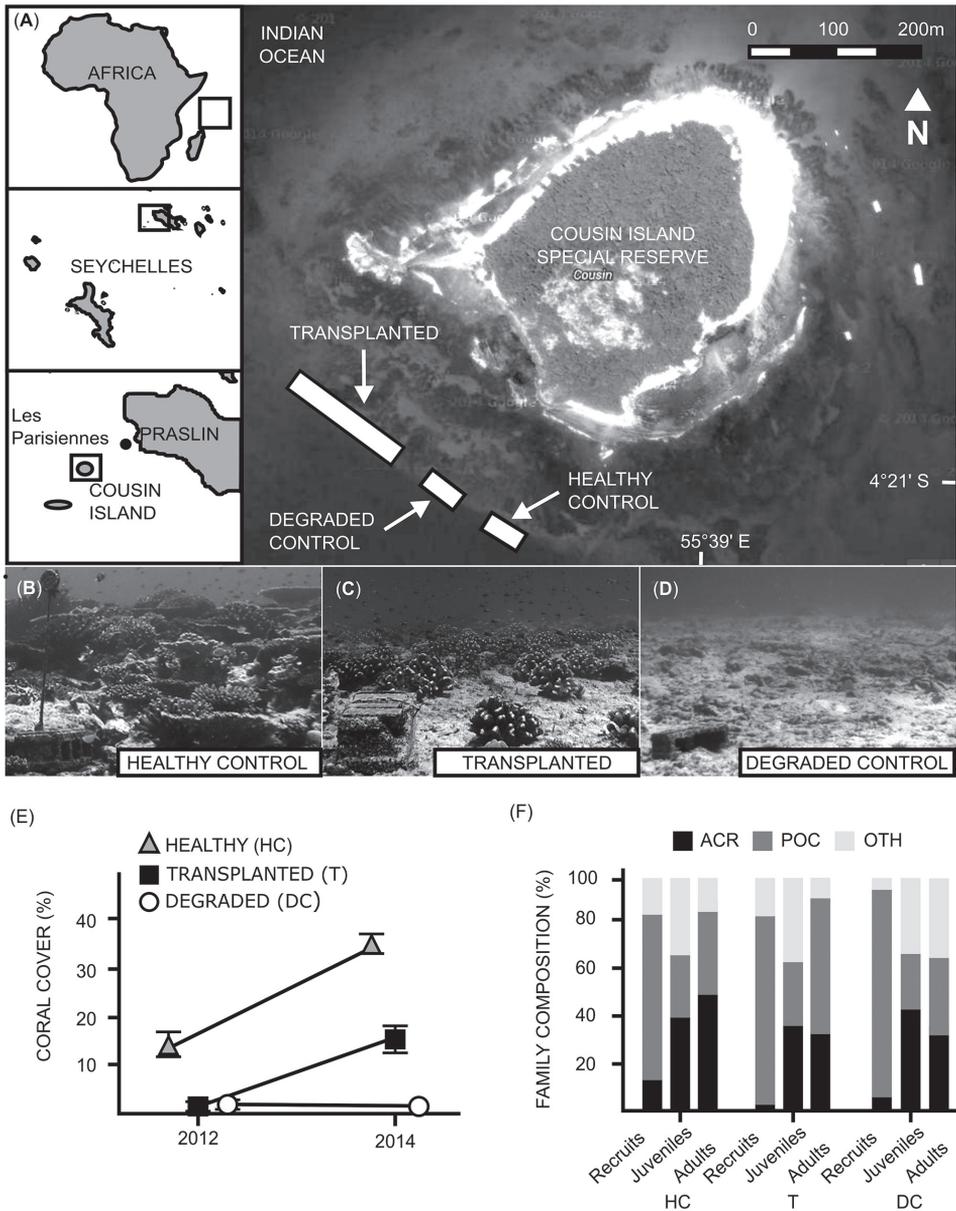


Figure 1. Study area and live coral cover and family composition at each site. **A** Locations of Seychelles, Cousin Island, donor site (Les Parisiennes) and the three study sites: healthy control, degraded control and transplanted. Lower panel shows the seascape and concrete blocks with tiles at **B** healthy control (HC) **C** transplanted (T) and **D** degraded control (DC) sites. **E** Change in average (\pm SE) live coral cover (% of total area) for individual sites between the start (November 2012) and the end (June 2014) of the transplantation project. **F** Family (ACR = Acroporidae; POC = Pocilloporidae; OTH = Other families) composition (% of total coral species) at three different stages (i.e. recruits, juveniles and adults) of the life cycle of corals in the three study sites at the end of sampling period. No significant differences in juveniles composition between sites or sampling periods were found.

the dominant transplanted coral genus was *Pocillopora*, which included one broadcast spawner (*P. grandis*) and two facultative brooding (*P. verrucosa* and *P. damicornis*) species (Schmidt-Roach et al. 2012 and references therein). All three study sites were separated by arbitrarily defined 50-m buffer zones. Figure 1 shows the 2012 and 2014 coral cover as well as the 2014 coral family composition for each site.

Our experience in the local conditions indicated strong ($\sim 0.5 \text{ m s}^{-1}$) bidirectional currents along the reef with no clear seasonal pattern due to local winds, tides and bathymetry (Jennings et al. 2000). From May to October the trade winds blow from the southeast (Southeast Monsoon), and from December to March they tend to blow from the northwest (Northwest Monsoon). The transition months of April and November have light and variable winds. The current and wind conditions suggest that all sites were equally exposed to two major environmental factors that affect coral settlement and recruitment, namely current patterns and connectivity to sources of coral larvae. We recognize that the differential post-1998 bleaching survivorship of the study area may suggest variations in microhabitat and small-scale oceanographic conditions between sites. However, we considered that any differences in environmental conditions between the transplanted and degraded sites were negligible because these two sites were similarly affected by the 1998 coral bleaching event and remained equally degraded prior to the start of the coral transplantation project in November 2011 (Figure 1). Further, Chong-Seng et al (2014) found that rates of coral recruitment to settlement tiles were similar across three different reef conditions (coral-dominated, rubble-dominated, and macroalgal-dominated reefs) in the inner Seychelles, suggesting that larval supply is not a limiting factor for reef recovery. Therefore, we assumed all three sites had the same likelihood of receiving coral larvae.

Coral recruitment

We deployed settlement tiles onto the reef between 9th and 15th January 2014, over 14 months after first coral transplantation. Based on our coral reproduction monitoring, this deployment schedule allowed approximately 3 weeks biological conditioning of the tiles prior to the first expected coral spawning in the area, the first week of February 2014 (Montoya-Maya, unpublished data).

Coral recruitment (spat <1 cm) was compared among all three study sites over a six-month period using settlement tiles. Two ceramic tiles (16 × 16 × 0.8 cm) were placed separately on a concrete block and secured with a plastic cable tie. Flat ceramic tiles attached to concrete blocks were used, rather than other more efficient coral settlement methods (e.g. tiles of differing texture and orientation; Petersen et al. 2005), due to the difficulty of sourcing local materials for more complex settlement structures. Although the results could provide an underestimate of total coral recruitment rates, we considered tile placement appropriate for our objectives. In January 2014, 20 concrete blocks, with two tiles per block, were deployed at each of the three study sites. All concrete blocks were deployed within the same depth range (8–10 m) with adjacent blocks

separated by 5 m. This deployment setup resulted in comparable survey areas (ca. 0.12 ha) at each site despite the transplanted site being larger. Tiles were retrieved in July 2014, >19 months after first transplantation. Tiles were left to dry in the sun for 24 hours and then rinsed in freshwater to remove sediments. Biofouling was insignificant and similar across sites, therefore, we considered unnecessary soaking the tiles in diluted bleach. Each tile was then visually examined twice by different observers using a stereomicroscope to identify coral spat. The coral spat were counted and identified to family level. Families of newly settled corals were identified following Babcock et al. (2003). Families that could not be identified due to damage or insufficient development were pooled into the category “unidentified”.

Coral juveniles

Coral juveniles were assessed four times: before transplantation, 12, 18 and 24 months after first transplantation. Abundance and diversity were quantified at genus level for coral juveniles by SCUBA diving and counting the number of juvenile scleractinian corals (<5 cm in diameter) within 1 m² quadrats on natural substrate. At the transplanted, degraded and healthy sites, six 10-m transects were deployed and within each transect three quadrats were randomly placed (using a random number table) for juvenile coral abundance. The substratum of each quadrat was carefully examined for non-fragmented small colonies. Any obstructive macroalgae was parted when necessary. Colonies resulting from fission, shrinkage or fragmentation of older colonies were excluded. Because individual corals were not being monitored through time and fixed quadrats were not used, estimates were considered as total number of juveniles (i.e. new juveniles and old juveniles) and not as an estimate of recruitment rates (i.e. number of new recruits per unit time).

Statistical analysis

The experimental design we used was a compromise between scientific objectives and the time required to implement a large-scale coral reef restoration project. We acknowledge the limitations such an approach has in our ability to statistically test the effect of the coral transplantation effort. Accordingly, differences in recruit and juvenile density between the three sites were evaluated using generalized linear mixed models (GLMMs) with a Poisson error structure, with the log link function and site as a fixed effect. There were two types of random factors. In recruit density, we used tile nested within cement block to account for pseudo replication. In juvenile density, we used time and quadrat nested within transects to account for pseudo replication and irregular monitoring intervals. We used the likelihood ratio (LR) test to determine the influence of fixed and random effects on recruit and juvenile densities by comparing the fit for models with and without the conditions (Bolker et al. 2009). When over-dispersion and excess of zeros were present in the data, a quasi-Poisson count variance structure with zero-inflated

models was used (Bolker et al. 2009; Harrison 2014). We completed the analyses for each of the two main transplanted families separately (Acroporidae and Pocilloporidae), for all other families pooled, and for all taxa pooled. All statistical tests were done in R (R Core Team 2013), for fitting GLMMs the *lme4* (v1.1-6; Bates et al. 2014) and *glmmADMB* (v0.8.0; Skaug et al. 2012) packages were used.

Results

Coral recruitment

During the six-month study, 326 spat were counted across all sites: 192 (58.9%) recruited on the upper surface of the tile and 134 (41.1%) settled on the sides. Pocilloporid corals predominated at all sites (80.7% of recruits) followed by other families (13.5%) and Acroporidae (5.8%). The average density was 2.8 ± 0.19 spat tile⁻¹ (86 ± 6.1 spat m⁻²) and ranged from 0 to 13 spat tile⁻¹ (0 - 351.4 spat m⁻²). Although the contribution of Pocilloporidae to the total number of spat at each site varied slightly (71.6-89.9%), the contribution of Acroporidae at the healthy site (12.6%) was higher than transplanted site (2.0%; Figure 1).

Total recruitment varied significantly among sites (LR test: $\chi^2 = 15.50$, $df = 2$, $P < 0.001$) and similar results were found for the three coral taxa examined (Acroporidae: $\chi^2 = 6.77$, $df = 2$, $P = 0.034$; Pocilloporidae: $\chi^2 = 11.2$, $df = 2$, $P = 0.004$; Other families: $\chi^2 = 12.10$, $df = 2$, $P = 0.002$). Spat density at the transplanted site was 1.6 times (0.46 ± 0.15 , $\beta \pm SE$ on the logit scale; Figure 2) higher than the healthy site (GLMM, $\zeta = 3.15$, $P = 0.002$; Table 1). Pocilloporid spat density at the transplanted site was 1.8 times higher (0.58 ± 0.18 , on the logit scale; Figure 2) than the healthy site (GLMM, $\zeta = 3.20$, $P < 0.01$). Although degraded site had consistently lower spat densities for all taxa examined, spat density from other than the two dominant families at the degraded site was significantly lower than the healthy site (GLMM, $\zeta = -2.15$, $P < 0.05$; Figure 2). Spat density at the transplanted site was higher than the degraded site for pocilloporids (GLMM, $\zeta = 2.52$, $P = 0.012$), other coral families (GLMM, $\zeta = 3.12$, $P = 0.002$), and all taxa combined (GLMM, $\zeta = 3.68$, $P < 0.001$), between 1.6 (Pocilloporidae) to 6 (Other families) times higher than degraded site (Table 1).

Coral juveniles

Throughout the four sampling periods between November 2012 and October 2014, 527 juveniles were counted in 216 quadrats. The overall juvenile density was 3.1 ± 0.19 juveniles m⁻², ranging from 0 to 16 recruits m⁻². Acroporid juveniles were 40.2% of the total coral juveniles across sampling periods, followed by other families (37.2%) and Pocilloporidae (22.6%). The family distribution of coral juveniles was similar between sampling periods and between study sites (Figure 1).

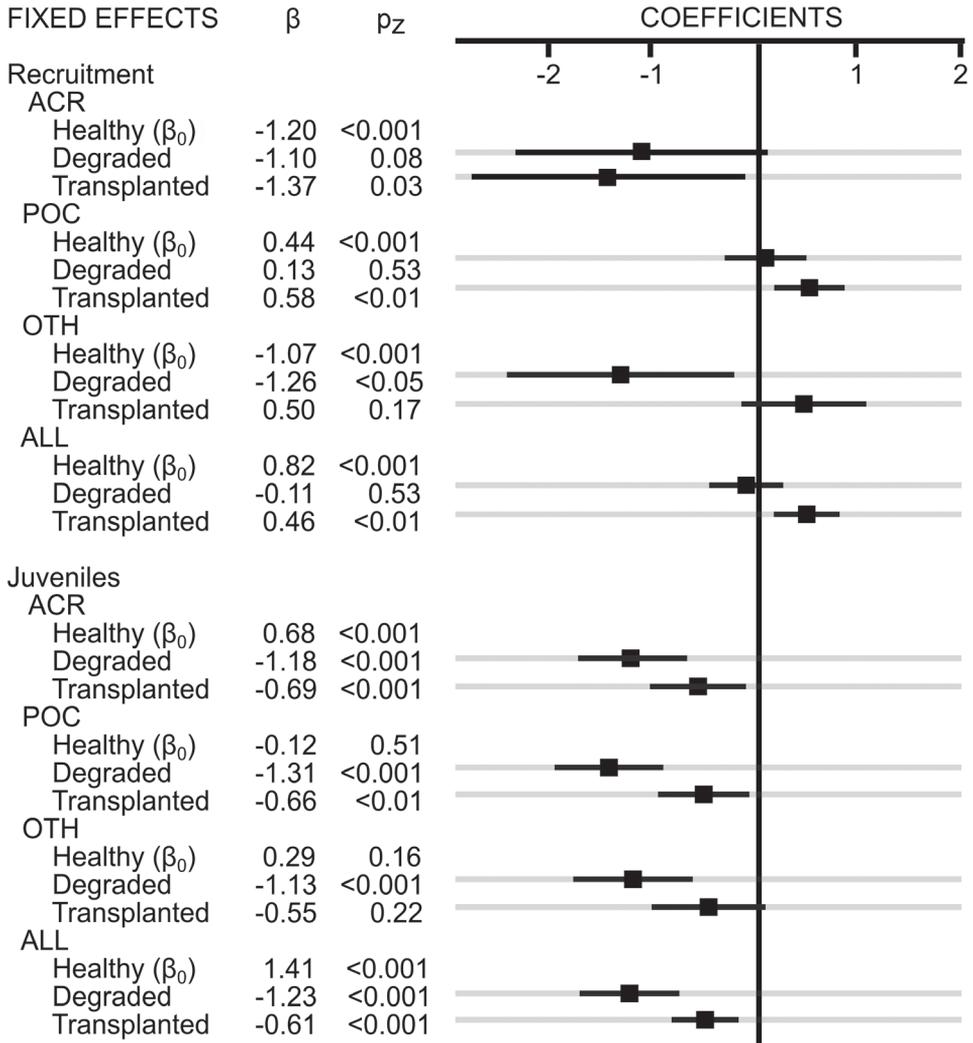


Figure 2. Estimated influence (marker) and 95% confidence intervals (lines) of each study site (DC– degraded control; HC – healthy control; T – transplanted) on coral recruitment and juveniles of acroporidae (ACR), pocilloporidae (POC), other coral families (OTH), and all individuals combined (ALL) based on poisson- distributed generalized linear mixed effect models (GLMMs). The HC site was set as the reference level (intercept). *A quasi-Poisson distribution family was set in the model to account for over dispersion.

Total juveniles varied among sites ($\chi^2 = 35.13$, $df = 2$, $P < 0.001$) and similar results were obtained for the three coral taxa examined (Acroporidae: $\chi^2 = 27.69$, $df = 2$, $P < 0.001$; Pocilloporidae: $\chi^2 = 23.48$, $df = 2$, $P < 0.001$; Other families: $\chi^2 = 18.73$, $df = 2$, $P < 0.001$). The healthy site had the highest total juvenile density (GLMM, $\zeta = 6.74$, $P < 0.001$; Table 1), particularly of Acroporidae (GLMM, $\zeta = 3.34$, $P < 0.001$; Figure 2). The

Table 1. Estimates of spat and juvenile densities (mean \pm SE) of Acroporidae, Pocilloporidae, other coral families (Other) and all families combined (All taxa) for each study site.

Taxon	Healthy Control	Degraded Control	Transplanted
Acroporidae			
Spat tile ⁻¹	0.3 \pm 0.08	0.1 \pm 0.06	0.1 \pm 0.04
Spat m ⁻²	9.7 \pm 2.61	3.3 \pm 1.95	3.3 \pm 1.30
Juvenile m ⁻²	2.1 \pm 0.24	0.7 \pm 0.16	1.0 \pm 0.19
Pocilloporidae			
Spat tile ⁻¹	1.7 \pm 0.22	1.9 \pm 0.22	3.1 \pm 0.43
Spat m ⁻²	55.4 \pm 7.17	61.9 \pm 7.20	101.0 \pm 14.01
Juvenile m ⁻²	1.4 \pm 0.18	0.4 \pm 0.09	0.6 \pm 0.11
Other			
Spat tile ⁻¹	0.4 \pm 0.04	0.1 \pm 0.06	0.6 \pm 0.13
Spat m ⁻²	13.0 \pm 1.30	3.3 \pm 1.95	19.5 \pm 4.23
Juvenile m ⁻²	1.6 \pm 0.16	0.5 \pm 0.11	1.1 \pm 0.21
All taxa			
Spat tile ⁻¹	2.1 \pm 0.24	2.4 \pm 0.22	3.8 \pm 0.41
Spat m ⁻²	68.4 \pm 7.82	78.2 \pm 7.17	123.8 \pm 13.35
Juvenile m ⁻²	4.8 \pm 0.40	1.7 \pm 0.26	2.7 \pm 0.38

Recruitment is expressed as both spat tile⁻¹ and no. spat m⁻². The latter represent standardized units.

degraded site had the lowest total juvenile density (GLMM, $\zeta = -6.36$, $P < 0.001$; Figure 2), particularly of Pocilloporidae (GLMM, $\zeta = -5.06$, $P < 0.001$; Figure 2). Juvenile density at the transplanted site was consistently higher than the degraded site (Acroporidae: GLMM, $\zeta = 2.06$, $P = 0.039$; Pocilloporidae: GLMM, $\zeta = 2.36$, $P = 0.019$; other families: GLMM, $\zeta = 2.12$, $P = 0.034$; all taxa: GLMM, $\zeta = 3.10$, $P < 0.01$; Figure 3), between 1.1 (Acroporidae) to 1.9 (Pocilloporidae) times higher than degraded site (Table 1). The time of sampling period had a significant influence on the juvenile density of all taxa ($\chi^2 = 10.28$, $df = 1$, $P < 0.01$) and Acroporidae ($\chi^2 = 6.83$, $df = 1$, $P < 0.01$); likely driven by a higher count of juveniles at the end of this study (Figures 3 and 4). However, the influence of sampling period on juvenile density was not statistically significant for Pocilloporidae ($\chi^2 = 0.55$, $df = 1$, $P = 0.457$) and other coral families ($\chi^2 = 1.94$, $df = 1$, $P = 0.164$).

Discussion

We quantified spatial differences in natural coral recruitment and juveniles after large-scale coral transplantation by comparing two untouched control sites (healthy and degraded) with the transplanted site. Coral recruitment was assessed >14 months after first transplantation using a single tile deployment. Six months after tile deployment, total spat density at the transplanted site was 1.8 times higher than the healthy site and 1.6 higher than the degraded site, but the magnitude of variation in coral recruitment between the transplanted site and the degraded site was up to 6 times for coral families other than Pocilloporidae and Acroporidae. Spatial variation in early coral

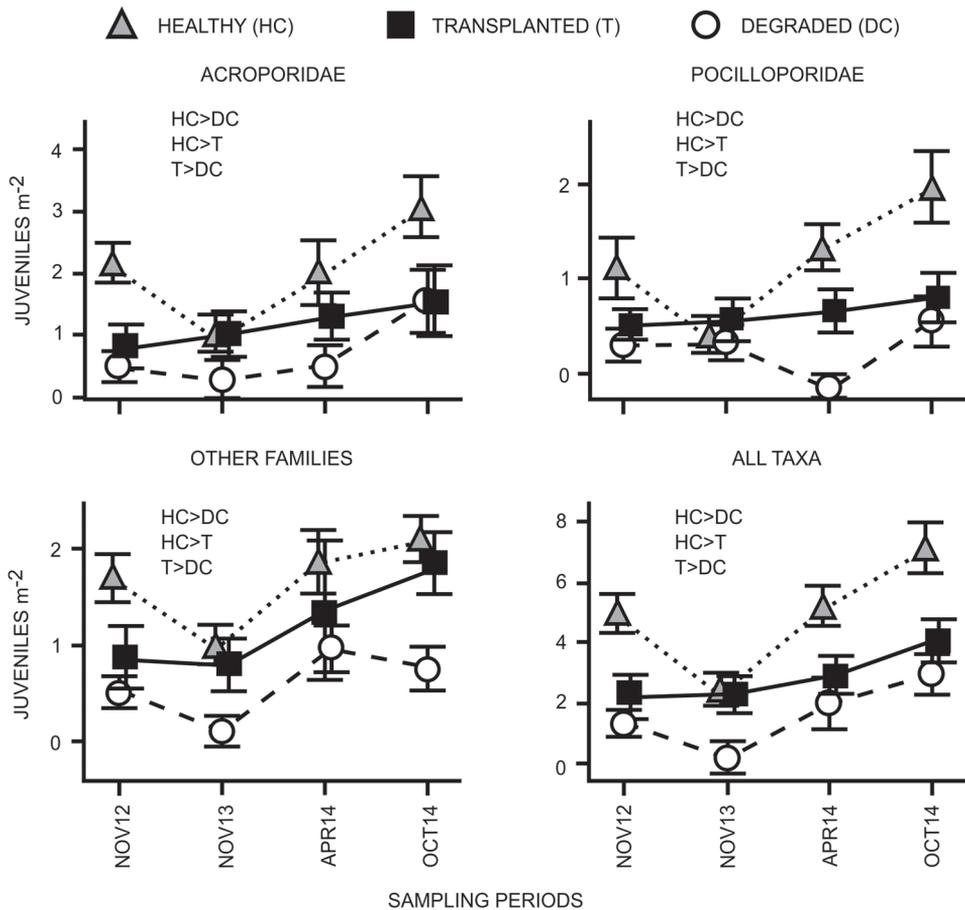


Figure 3. Mean (\pm SE) numbers of juveniles observed at the three study sites by sampling period. Data are presented for all individuals combined and for Acroporidae, Pocilloporidae and other families separately. Dates correspond to the four sampling periods. Statistical significant differences ($P < 0.05$) between sites are also shown.

recruitment is common between and within reefs (Fisk and Harriot 1990; O’Leary and Potts 2011). The variation at larger scales has been explained by differences in habitat quality, represented by differences in adult cover and substrate composition (Vermeij 2005), whereas at smaller scales it has been related to fish grazing and predation (O’Leary and Potts 2011). Coral transplantation clearly results in the modification of coral cover and substrate composition at the transplanted site (Edwards and Gomez 2007; Frias-Torres et al. unpublished data). Therefore, it is possible that the changes in habitat quality resulting from large-scale coral transplantation promote coral recruitment at the transplanted site.

We propose three reasons to explain the increase in coral recruitment at the transplanted site. First, the transplanted corals increase local production of coral larvae.

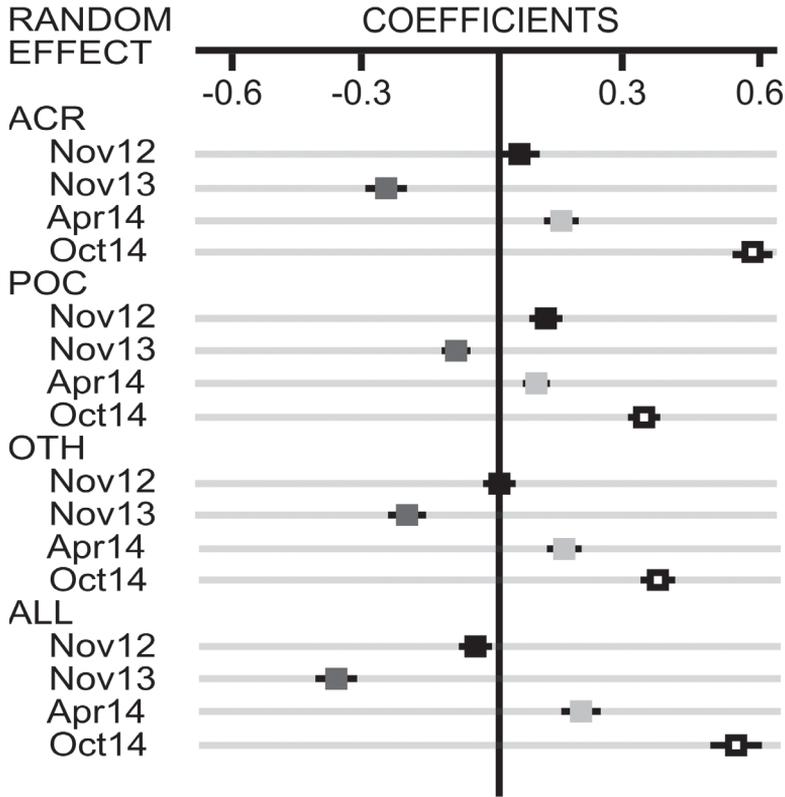


Figure 4. Estimates of the effects of sampling period on coral juveniles across the three sampled sites. Estimated coefficient (marker) and 95% confidence intervals (lines) are shown for all individuals combined (ALL) and for acroporidae (ACR), pocilloporidae (POC) and other families (OTH) separately.

The transplanted colonies were large enough at transplantation time (>15 cm) to have a high probability of being mature (Babcock 1991; Montoya-Maya et al. 2014) and there were gravid colonies at the transplanted and healthy sites (P. H. Montoya Maya, personal communication, February 2014). It is possible that the majority of larvae settling at the transplanted site were locally produced by the dominant transplanted coral genus *Pocillopora*. This genus included brooding species with larvae that can settle very close to parental colonies (Gorospe and Karl 2013). Second, the transplanted site attracts more coral larvae from elsewhere due to an increase in settlement cues. The transplanted site has an area three times larger than the two control sites (Figure 1), high species diversity and coral cover. These conditions may offer more available space and signal more favorable settlement, survival and growth conditions to incoming coral larvae (Kingsford et al. 2002; Sponaugle et al. 2002; Vermeij 2005; Edwards and Gomez 2007; Suzuki et al. 2008; Nakamura and Sakai 2009; Dixon et al. 2014) compared to the healthy and degraded sites. The higher recruitment of acroporids at the healthy site and of pocilloporids at the transplanted site - where their respective

coral cover (Figure 1) and adult densities are higher (Frias-Torres et al. unpublished data) – also add support to this statement. The lower number of total recruits at the healthy site, where coral structure is better, may be explained by an increase in recruit mortality from fish predation and grazing (O’Leary and Potts 2011) due to having a more diverse fish community than the two other sites (Frias-Torres et al. unpublished data). Further, a positive relationship between adult cover and recruitment rates (spat tile^{-1}) was found for pocilloporids in the Inner Seychelles (Chong-Seng et al. 2014). Enhanced settlement cues at the transplanted site due to the large-scale nature of the restoration project explain the overall higher number of coral spat and the higher number of spat from non-transplanted families compared to the degraded site. Third, both self-recruitment and attraction from elsewhere increased overall recruitment at the transplanted site. Such interaction of self-recruitment and attraction to increase coral recruitment has been suggested at a previous coral restoration study in Kenya (Mbije et al. 2013). We suggest future research could use techniques to identify immigrant and locally produced spat (e.g. assignment tests, Broquet and Petit 2009) to determine the real effect coral transplants have in local seeding or larval attraction from elsewhere.

Coral juveniles were assessed over a 2-year period that included sampling before and after coral transplantation. Total juvenile density and that of the three taxa examined was highest at the healthy site, intermediate at the transplanted site and lowest at the degraded site. Juvenile density at the transplanted site was consistently higher than the degraded site: between 1.1 (Acroporidae) to 1.9 (Pocilloporidae) times higher. Structural complexity is related to higher recovery rates due to enhanced recruit survival (e.g. indirectly reduces competition with algae and erosion by urchins or loose rubble; Graham and Nash 2013). This explains the higher recruit density at the healthy site (high structural complexity) compared to the transplanted site (medium structural complexity) and the higher juvenile density of the healthy and transplanted sites compared to the degraded site (low structural complexity; Jörgensen et al 2015). Similar results were obtained when comparing coral recruitment between high-, intermediate-, and low-quality zones in Florida (Vermeij 2005). Alternatively, natural recovery of the reefs in the inner Seychelles is ongoing (see Graham et al 2015) and the healthy site compared to the other two sites is leading the way as it is an “older” reef which has been accumulating small corals for longer. Nevertheless, coral transplantation may help in accelerating natural recovery of a degraded reef by improving its structural complexity. This will explain the differences in the number of coral juveniles between the transplanted and degraded sites, and the steady uptrend in the density of coral juveniles at the transplanted site over the sampling period when compared to the other two sites. Therefore, physical (e.g. varying sizes and growth forms of coral transplants on sites) and biological (e.g. including fish, snails and any other reef organism known to help coral recruit survival) complexity should be promoted in reef restoration projects to enhance the survival of settlers (Biggs 2013). In addition, in future studies it would be valuable to include a measure of complexity (e.g. rugosity) to evaluate coral settlement and recruitment on transplanted sites with varying levels of structural complexity.

The healthy-degraded-transplanted site cluster lacks replication at multiple locations and multiple times which limits the generalization of our results (Underwood 1993). Therefore, other alternative explanations to our results should be considered. One alternative is that the differences observed in coral settlement and recruitment among the sites existed prior to coral transplantation. A second alternative to consider is differential larval supply to the three sites. Although the sites are part of a single fringing reef, the healthy and transplanted sites are located at opposite ends of the reef which could result in differences in connectivity to source reefs. We found these two alternatives unlikely because there were similar estimates of coral spat between the two reference sites and there were similar number of juveniles between the transplanted and degraded sites before transplantation. In addition, coral juveniles at the transplanted site showed a constant uptrend in contrast to the up- and downtrend seen at the healthy and degraded sites (Figure 3). Finally, spatial variation in coral settlement and recruitment in the inner Seychelles has not been linked to differences in larval supply, which results in similar rates of coral settlement between reefs of different habitat quality (Chong-Seng et al. 2014). The lack of replication in our study hinders our ability to rule out completely all alternative explanations. We found the most parsimonious interpretation is that the transplantation of nursery-grown corals onto the degraded site resulted either in the attraction or the production (or both) of more coral larvae than the two control sites (healthy and degraded), with a higher chance of survival of settled corals at the transplanted site than at the degraded site. Even with its limitations, this study shows that the large-scale coral restoration effort in Seychelles assisted the natural recovery of the transplanted reef.

Our results are consistent with conclusions and best practices outlined in previous studies of coral reef restoration for species selection and transplant substrate. The use of brooding species in reef restoration projects is seen as a particularly effective form of transplantation (Rinkevich 1995; Edwards and Clark 1999). Our high spat density from the dominant transplanted family, Pocilloporidae, supports this. We cemented coral transplants directly onto denuded reef areas without the use of artificial structures, which allowed corals to self-attach 1-2 months post-cementing. Such technique may have increased survival of coral transplants, which further enhanced coral settlement and recruitment. Similar results were obtained by Mbije et al (2013) in Tanzania when transplanting corals onto denuded reefs without the use of artificial structures. Artificial structures in reef restoration projects increase transplant mortality due to their instability and the shorter lifespan of the structure (Clark and Edwards 1995; Ferse et al. 2013), and decrease abundance and diversity of coral recruits at restoration sites (Biggs 2013).

The effects of project size, duration and location should also be considered. Increasing the size of the transplanted area and expanding the monitoring time are required to observe any positive effects of active reef restoration (Edwards and Gomez 2007; Normile 2009). The number of corals and size of area transplanted make our project the largest reef restoration effort completed to date (Clark and Edwards 1995 Ferse et al. 2013; Mbije et al. 2013). An upward trend in coral recruitment was evident in our study with modeled coefficients of time effects consistently higher 24 months

after transplantation. Similar results were observed by Ferse et al. (2013) 14 months after transplantation in Sulawesi, Indonesia, for settlement of Acroporidae and Pocilloporidae. It is possible that previous projects were too small to cause a positive influence on coral recruitment, or the monitoring time period was too short to observe any effects. Project location is critical to detect the signal of increased coral settlement and recruitment. Our project was carried out within a no-take marine reserve where human stressors that can interfere with natural reef recovery were controlled. Therefore, our results support the application of large-scale, science-based coral reef restoration projects with at least a three year monitoring time-scale to assist the recovery of damaged reefs within protected areas.

Our approach confirmed the hypothesis that scleractinian coral recruitment and juveniles will be higher at the transplanted site than at the degraded site. As coral reefs continue to degrade, it is imperative that we understand how active reef restoration impacts natural reef recovery. We have shown coral transplantation with colonies large enough to be reproductive results in higher structural complexity, self-recruitment and recruitment of non-transplanted species. These results confirm coral reef restoration can be sustainable in the long-term. Enhanced natural coral settlement and recruitment resulting from coral transplantation holds great promise for the success and long-term sustainability of large-scale coral reef restoration, at least for those projects aimed at assisting the recovery of naturally degraded reefs in the Seychelles.

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Analysing fragmentation in vulnerable biodiversity hotspots in Tanzania from 1975 to 2012 using remote sensing and fragstats

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Abstract

Habitat fragmentation is a threat to conservation of biodiversity hotspots in the Morogoro region, Tanzania. However, on-going research on fragmentation has not kept pace with temporal lapses and how individual species respond to habitat transformation and heterogeneity. This study sought to model spatial and temporal fragmentation patterns. Cloud free multi-temporal Landsat imagery with similar spectral resolution were acquired in the same season in 1975, 1995 and 2012. The images were used to characterize the biophysical landscape characteristics and a range of metrics used to quantify the magnitude of fragmentation. Patches and classes in the landscape were assessed using Fragstats, a spatial statistics program useful in computing landscape metrics. Results show that patch number was higher in dense forest and woodland than in less dense forest and grassland in 1975, 1995 and 2012 while the interspersed juxtaposition Index (IJI) ranged between 0 (for clumped patches) and 100 (for grassland). In 1975 and 1995, the grassland habitat had the highest IJI while in 2012 less dense forest had the highest IJI. The Games-Howell test showed a significant fragmentation trend in less dense forests class ($p \leq 0.05$). Generally, the study indicates a high fragmentation pattern in the vulnerable tropical eastern arc mountain region of East Africa. This finding demonstrates the value of remotely sensed data in understanding the impact of anthropogenic processes on natural landscape transformation. Furthermore, the study provides a basis for informed conservation policy design and implementation in the region.

Keywords

habitat, fragmentation, fragstats, remote sensing, Tanzania

Introduction

Habitat fragmentation, an indication of habitat transformation, degradation and loss is a great concern globally (Fahrig 2001, Fahrig 2003, Cushman et al. 2010, Forman and Godron 1986). It refers to habitat breakages or the degree of patchiness of a habitat, mainly as a result of anthropogenic impacts (Fahrig 2001, Fahrig 2003, McGarigal and Cushman 2002, Wiens 1995, Neel et al. 2004). Generally, habitat fragmentation interferes with the structural configuration of ecosystems and their ecological functioning (Abdullah and Nakagoshi 2007, Echeverria et al. 2006, Echeverria et al. 2008, Iida and Nakashizuka 1995, Forman and Godron 1986). Specifically, fragmentation reduces total habitat area, making species highly vulnerable to endemism and extinction (Yen et al. 2005, Murcia 1995, Aguilar et al. 2008, Yen et al. 2005). Hence fragmentation has long term impacts on species numbers (Aguilar et al. 2008) and species abundance (Fahrig 2003, Debinski and Holt 2001, Yen et al. 2005, Forman and Godron 1986) as it exposes natural ecosystems to external risks such as parasitism and dominance of invasive species (Wiens 1995).

Habitat fragmentation is an explicit challenge to conservation in the tropics (Vogelmann 1995). It is considered a major cause of species loss (Pelkey 2000, Adams et al. 2003, Bjørndalen 1992, Burgess et al. 2002, Burgess et al. 2001, Yen et al. 2005, Forman and Godron 1986). In Africa, approximately 310,000 hectares of forest is annually converted to agriculture, while 200,000 hectares is converted into woodlands, major causes of fragmentation (Achard 2002). Fragmentation acts synergistically with other factors like effects of solar radiation and open niches that lead to dominance of other invasive species. Consequently, native vegetation species are exposed to higher risks of extinction with a decline in the percentage area required for their survival (Rutledge 2003).

Ecosystems in Morogoro region, Tanzania contribute to the world's climate regulation through large carbon stores (Burgess et al. 2007, Swetnam et al. 2011). These forests are also characterized by high levels of endemism and many species are vulnerable to extinction (Swetnam et al. 2011, Brooks et al. 2006, Myers et al. 2000). Increased anthropogenic disturbances in particular pose significant threats to their long term conservation (Hall et al. 2009, Hall 2009, Newmark 1998). Between 1955 and 2000 for instance, forest cover declined from 300 km² to 220 km² (Burgess et al. 2007). Despite the area's global importance, few studies have been conducted with a focus on its spatial heterogeneity (Newmark 1998). Furthermore, mechanisms by which natural habitats respond to spatial heterogeneity across diverse fragmenting ecosystems remain largely unexplored (Swetnam et al. 2011, Yanda and Shishira 1999). Individual habitats may differ in their degree of response to fragmentation as the robustness of fragmentation may vary (Fahrig 2003, Neel et al. 2004, McGarigal 2006,

Echeverría 2007). For instance, due to differences in their structural complexity and biological processes, what could be termed as fragmentation in homogeneous landscapes may be interpreted differently in a heterogeneous landscape (Murcia 1995, Fischer and Lindenmayer 2007, Wiens 2000). In this study, we tested the spatial extent and magnitude of fragmentation in four vulnerable habitats subjected to fragmentation in the region. Remote sensing was applied due to its increasing popularity in quantifying spatio-temporal patterns in diverse landscapes (Ojoyi et al. 2016, Nagendra et al. 2004, Lung and Schaab 2006, Southworth et al. 2002, Fjeldså 1999). Specifically, the study pursued the following objectives: (1) to investigate multi-temporal magnitude of fragmentation in diverse habitats; (2) to quantify the intensity of habitat fragmentation in each of the habitats.

Study area

Similar to this case study, most rich biodiversity hotspots in Tanzania are geographically located in the Eastern Arc Mountains (Burgess et al. 2007, Myers et al. 2000, Hall et al. 2009, Hall 2009, Newmark 1998, Olson and Dinerstein 1998). In this study, we selected a section of Morogoro region dominated by four major habitat types (Figure 1). The choice of the study location was based on previous ecological studies (e.g. Burgess et al. 2002, Burgess et al. 2001, Hall 2009, Luoga et al. 2000, Yanda and Shishira 1999) that attributed species losses to fragmentation. The study area is characterized by sub-montane (with trees 30-50m tall), montane (with trees 15-30m tall) and upper montane (with trees 15-20m tall) forest at 1200-1500, 1500-2100 and >2100m asl, respectively. Generally, forest density and height varies with elevation and aspect, with dense canopy dominating lower altitude and elfin forests dominating ridges above 1900m asl (Lovett et al. 1996). Stunted grass patches are also common at high altitudes. According to Burgess et al. (2002), the potential of closed natural forest cover is about 500km², however, this has been reduced from 300km² in 1955 to 230 km² in 2001, with most decline recorded at 600-1600 m asl outside protected areas. The loss is mainly attributed to increasing population growth, estimated at about 2.5-3% per annum (Lovett 1996). The study area comprises four main habitats; woodland, dense forest, less dense forest and grassland. In this study, woodland is described as woody vegetation with scattered foliage cover (less than 30%) with mature stands of less than five meter tall while less dense forest consists of fields and patches with trees of more than six meters tall, with crown cover of less than 30%. The dominant tree species in the region include: *Bersama abyssinica*, *Cassipourea malosana*, *Cornus volkensii*, *Cussonia lukwangulensis*, *C. spicata*, *Dombeya torrida*, *Draceana afromontana*, *Garcinia volkensii*, and *Xymalos monospora*. Bamboo thickets form dense stands of *Sinarundinaria alpina* 12-15 m tall and 15 cm diameter (Bjørndalen 1992, Shirima et al. 2011, Lovett 1993). The grassland habitat consists of *Panicum lukwangulense* and *Andropogon thytinus* with scattered trees of *Agauria saliciflora*, *Adenocarpus mannii*, *Myrica salicifolia* and *Berberis* sp. thought to have replaced upper montane forest due to fires (Adams et al.

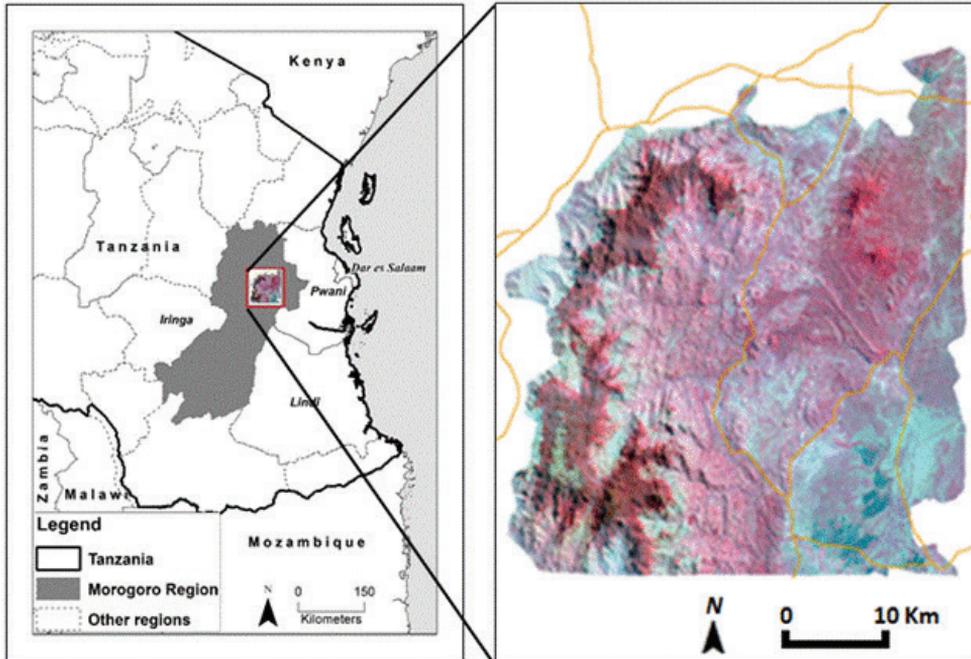


Figure 1. A 1975 Landsat composite overlaid on the study area.

2003, Bjørndalen 1992). Kitulanghalo forest is located between Morogoro and Dar es Salaam within Morogoro region. The woodland forms part of Miombo woodland which covers 90% of the total forested ecosystem (Mugasha et al. 2013, Munishi et al. 2010). It is dominated by *Brachystegia*, *Isoberlinia*, *Julbernardia*, *Pterocarpus angolensis*, *Azelia quanzensis* and *Albizia species* (Chander 2009). The area falls within a semi-natural Miombo woodland which receives less than 1000 mm of rainfall per annum. Their proximity to Morogoro urban area increases their susceptibility to anthropogenic activities, altering their functioning and sustainable management (Mugasha et al. 2013).

Methodology

Image pre-processing

Landsat MSS (20/08/1975), Landsat TM (30/09/1995) and Landsat ETM+ (20/07/2012) imagery with better visualization (less than 15% cloud cover) from the Global Landcover Facility (<http://www.landcover.org>) were selected for the study. Datum was set to WGS 84 and referenced to Universal Transverse Mercator (UTM) zone 37 South. All images were orthorectified using ground validation points, Digital Elevation Model (DEM) and aerial photos as a reference. Landsat images were resampled to a common resolution pixel (30 × 30 m) using bilinear resampling to ensure consistency

in all image scenes. First order polynomial transformation was applied at image registration to correct for any shifts. It was deemed necessary to simulate atmospheric interactions between the sun and sensor pathways for the imagery used. Therefore, a radiative transfer model in Atmospheric and Topographic Correction (ATCOR) module in Erdas Imagine 2013 was used for atmospheric correction. ATCOR masks haze, cloud, water and enhances pixel visibility. In this study, we used the MODerate resolution atmospheric TRANsmission (MODTRAN) code to retrieve the atmospheric parameters for ATCOR from the look-up table as ground-based reflectance and atmospheric data were unavailable. Digital number values were then converted to reflectance based on metadata provided with the Landsat images (Chander et al. 2009, Guanter et al. 2009, ERDAS and Geosystems 2011).

Image classification

A supervised maximum likelihood classifier was adopted for classification (Liu et al. 2002, Manandhar et al. 2009, Tseng et al. 2008, Xi 2007). The technique is based on statistical probability that assigns pixel values to the category with the highest likelihood (Aldrich 1997, Dean and Smith 2003, Ince 1987). Spectral signatures were created and applied in categorizing similar pixels in the entire image using eight polygons representing training data sets for each habitat class. A color composite of 3, 4 and 5 bands were used to facilitate visual interpretation while the Gaussian distribution function was applied in the stretching process. The image was classified into four class categories namely: Woodland, Grassland, Dense forest and Less dense forest. A total of 82 field ground data points, archival high resolution aerial photographs, interviews and expert opinion were used to validate the classified images. Confusion matrices were then created to compare reference data with the maximum likelihood prediction and for calculation of the overall accuracy (OA), producer's accuracy (PA) and user's accuracies (UA). Overall accuracy is a percentage (%) between correctly classified classes and the total number of test reference data, while producer's accuracy is the probability of a specific class being correctly classified. User Accuracy is the possibility that a sample of a specific class represents the category on the ground.

Modelling habitat fragmentation

Fragstats metrics were extracted from all processed Landsat images. Fragstat metrics offer a distinct capacity to determine a landscape's spatial configuration, hence valuable in understanding landscape change arising from fragmentation (Cushman 2006, Jorge and Garcia 1997, Saikia et al. 2013, Millington et al. 2003). All classified images were converted to ASCII format in ArcGIS 10.2. A C-program, a raster version inbuilt within Fragstas that accepts ASCII image files was applied using the eight cell rule. The ASCII format scenes were imported into Fragstats and ASCII built-in-algorithm se-

Table 1. Fragmentation Indices used in the current study.

Fragstats Metrics	Description
Patch Density (PD)	Number of patches of the corresponding patch type.
Largest Patch Index (LPI)	An index used to quantify the percentage of total landscape area characterized by the largest patch.
Edge density (ED)	Used to assess edge length per unit area.
Patch Number (NP)	A measure of the magnitude of fragmentation of patches
Interspersion Juxtaposition Index (IJI)	A measure of adjacency of patches determined by dividing the length between patch edge by the number of patches within a landscape. Values approaching 0% indicate that a patch is adjacent to only one other patch and 100% indicate that a patch is in similar proximity to multiple patches within a landscape.
Patch Area (MN)	The sum across all patches in the landscape of the corresponding patch metric values, divided by the total number of patches. Expressed in hectares.
Perimeter Area Ratio- PARA	Refers to the ratio of the patch perimeter (m) to area (m ²).
Total Area (CA)	Refers to the sum of areas (m ²) of all patches for the patch type.
Percentage of Landscape (PLAND)	Useful in computing the proportional abundance for each of the patch type across the landscape.

lected for running the Fragstats model. Three multi-level structure metrics were selected at patch, class and landscape level (McGarigal and Cushman 2002). Metrics relevant in explaining the magnitude and extent of fragmentation were then selected from the 1975, 1995 and 2012 image scenes. A total of 155 samples were randomly selected and extracted. As recommended by McGarigal and Cushman (2002) two metrics i.e. perimeter area relationship and patch area were statistically used to test the magnitude of fragmentation. Mann-Whitney U and Post hoc ANOVA tests were used to evaluate differences among patch areas in all the years. The Games-Howell was used to determine forest fragmentation. The indices used in this study are briefly described in Table 1.

Results

Classification and accuracy assessment

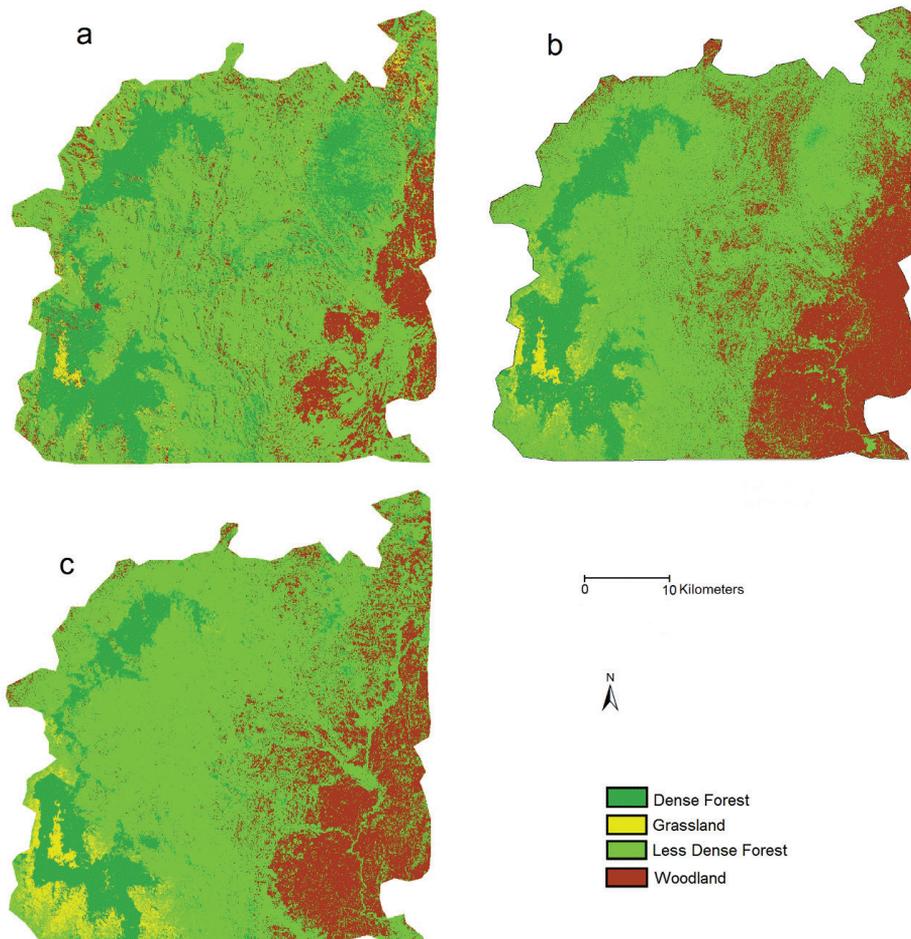
The overall accuracy for 1975, 1995 and 2012 image scenes was 78.26%, 84% and 76.54% respectively (Table 2). Changes in total area coverage were observed in all years (Figures 2a, b and c).

Change detection

The study findings showed substantial land modification in most of the cover types during the study period i.e. decline in dense forest (31, 675.70 hectares) and less dense forest (by

Table 2. Accuracy assessment tests (Producer's Accuracy - PA), User's Accuracy - UA).

Habitat Class	1975		1995		2012	
	PA (%)	UA (%)	PA (%)	UA (%)	PA (%)	UA (%)
Dense Forest	100	75	100	100	80.77%	95.45%
Less Dense Forest	66.67	100	100	100	100.00%	60.00%
Woodland	66.67	100	66.67	66.67	75.00%	58.54%
Grassland	100	100	100	100	84.62%	91.67%
Overall Accuracy	78.26		84		76.54%	
Kappa co-efficient	0.7416		0.812		0.7284	

**Figure 2.** Land use land cover (LULC) maps in 1975 (a), 1995 (b) and 2012(c).

11, 267.38 hectares) and increase in grassland (21, 230.01 hectares). However, changes in areas covered by woodland were inconsistent, i.e. increase by 15,884.46 hectares between 1975 and 1985 and decline by 8, 182.03 between 1985 and 2012) – Figure 2.

Fragmentation trends

Temporal variability in fragmentation

Dynamic fragmentation trends were observed (Table 3). Patch number was relatively higher in dense forest and woodland in 1975, 1995 and 2012 than in less dense forest and grassland. The highest percentage of landscape (PLAND) were recorded in less dense forest than the rest of the habitats while woodland and less dense forest habitats had the highest edge density (Figure 3a–c). Furthermore, dense forest showed the most declining patch number during the study period. An analysis of the largest patch index (LPI) showed that less dense forest had the highest LPI, while woodland, dense forest and grassland had the least values, below five. Woodland had the highest PARA compared to the rest of the habitat types (Table 3).

Spatial variation in fragmentation

Study findings indicated a higher probability of dispersion linked to woodland and less dense forest. Interspersion Juxtaposition Index (IJI) ranged between 0 (for clumped patches) and 100 (for grassland). In 1975 and 1995, the grassland habitat had the highest IJI while in 2012, less dense forest had the highest IJI. The interspersion juxta-

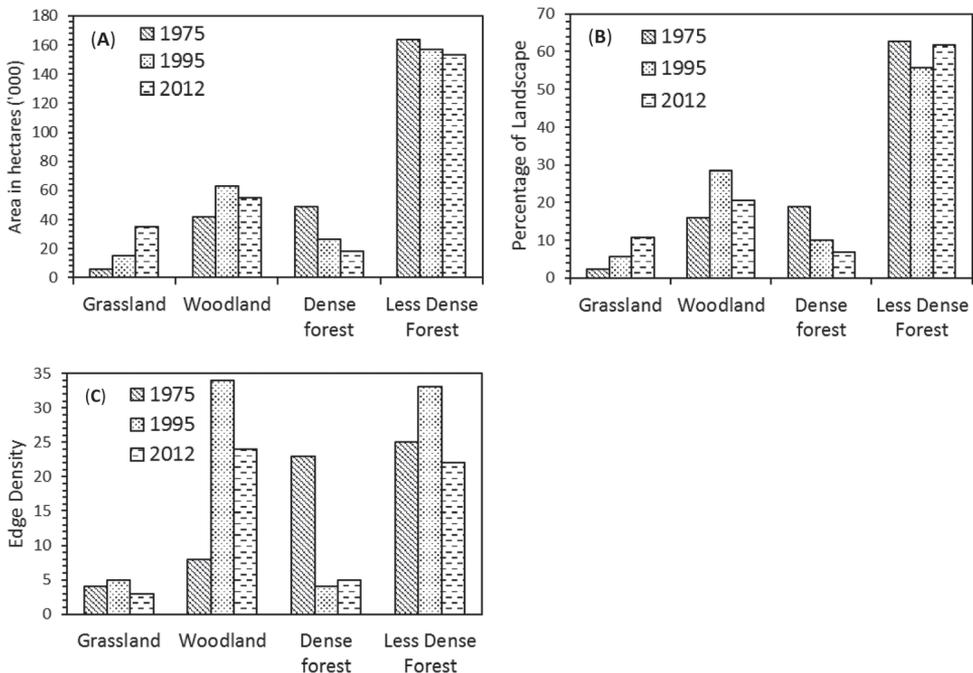


Figure 3. Temporal patterns of total area coverage (A), percentage of landscape (B) and edge density (C).

Table 3. Patch area compared by Mann-Whitney Tests.

Class	Year	z-value (1975–1995)	Prob > z	z-value (1995–2012)	Prob> z
Dense forest	1975	9.495***	0	-6.872	0.1895
	1995				
	2012				
Grassland	1975	13.680***	0	-7.441***	0
	1995				
	2012				
Less dense forest	1975	16.728***	0	-8.268***	0
	1995				
	2012				
Woodland	1975	-16.63***	0	2.461***	0
	1995				
	2012				

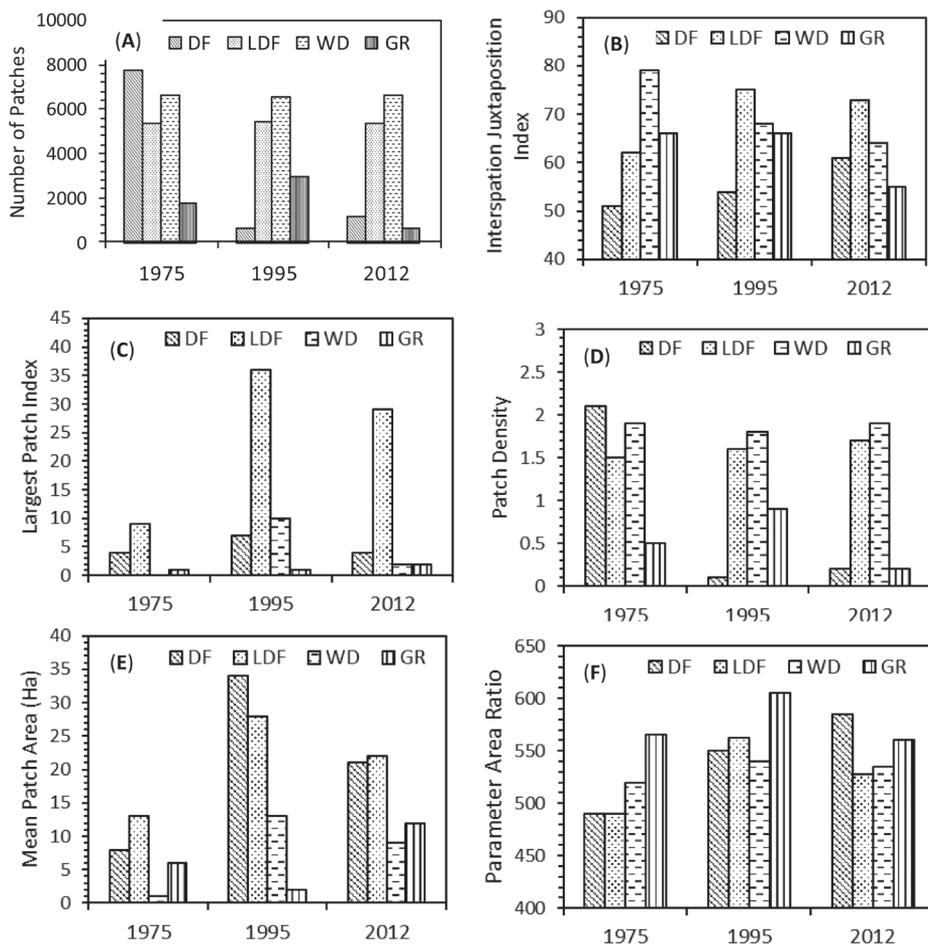


Figure 4. Spatial variability in number of patches (A), Interspersion Juxtaposition Index (B), Largest patch index (C), Patch density (D), Mean patch area (E) and Perimeter area ratio (F) in 1975, 1995, and 2012. DF- dense forest, LDF-less dense forest, WD-woodland, GR-grassland.

position index (IJI), was useful in characterizing the degree of adjacency for each patch type e.g. Burgess et al. (2007). Additionally, the largest patch number and mean patch area was evident in dense forest in 1975 and woodland in 2012 (Figure 4).

Mann-Whitney test results

Mann-Whitney tests were applied to the data. Mann-Whitney test results showed distinct differences in patch area ($p < 0.01$) as summarized in (Table 3). These results were strong indicator of a rapidly fragmenting landscape.

Games Howell test results for perimeter area relationship

Game-Howell test is ideal for unequal sample sizes characterised by heterogeneity and has been widely used in vegetation mapping that include taxonomic profiles in the Atlantic and Caatinga biomes of northeastern Brazil (Pacchioni et al. 2014), forest transformation in Uluguru mountains (Ojoi et al. 2015), the effect of fire on Penderosa pine forest density, canopy cover, tree size and basal area (Stephens et al. 2015) and shrub density in Zegros forest, southwest Iran (Askari et al. 2013). Games Howell test results showed significant patterns of fragmentation between 1975 and 1995 in all habitats ($p \leq 0.05$). In 1975 and 2012, the trend was significant in less dense forest and woodland ($p \leq 0.05$), while in 1995 and 2012, the trend was significant in grassland, dense forest and less dense forest ($p \leq 0.05$) (Table 4). A highly significant trend with perimeter area relationship was evident with less dense forest across the years.

Discussion

This study showed a progressive fragmentation at both spatial and temporal domains. Variability in responses to fragmentation was also noted for different habitats. Fragmentation in the area is not only dependent on topography but also adjacency to land for agriculture, urbanization/settlement and infrastructure development, which

Table 4. Games-Howell tests for the mean parameter area ratio (PARA) in 1975, 1995, 2012.

Class	Mean			<i>p</i> value		
	1975	1995	2012	1975 vs 1995	1975 vs 2012	1995 vs 2012
Grassland	565.28	606.21	560.00	0.0001	0.596	0.0001
Dense forest	498.12	549.14	483.7	0.0001	0.3	0.0001
Less dense forest	496.29	563.06	529.5	0.0001	0.0001	0.0001
Woodland	498.58	535.43	534.3	0.0001	0.0001	0.893

are considered key drivers of landscape transformation in the region. All these anthropogenic activities contribute to habitat losses and species decline. Implications on the landscape are presented with a reflection on policy and future management.

Habitat modification

There was a transformation in habitat extents within the study area. Significant losses were recorded for dense forest (31, 675.70 hectares) and less dense forest (by 11, 267.38 hectares), however, there was a steady increase in areas covered by grassland. Based on field study observations, these changes can be attributed to expanding agricultural fields and increased exploitation of timber and non-timber products to meet the increasing urbanization demand in Morogoro district. This finding is in agreement with Burgess et al. (2001) and Burgess et al. (2002) who found a substantial decline of dense forest in the Uluguru mountains due to urbanization and agricultural (Burgess et al. 2002, Burgess et al. 2001). In other parts of Tanzania, related studies established effects of reduced tree density to land modification (Yanda and Shishira 1999, Muniishi et al. 2010). Habitat modification could also be attributed to general population increase in non-urbanized areas, also known to influence its spatial configuration (Fischer and Lindenmayer 2007).

Spatial and temporal variation

As aforementioned, there was a general decrease in area covered by dense and less dense forest habitat. A decreasing trend in the extent of total habitat coverage relates to deleterious fragmentation as effects of habitat fragmentation are dependent on habitat size (Fahrig 2003). Furthermore, perimeter-area results in this study show distinct differences in woodland and grassland habitats. In most instances, high perimeter-area relationship characterizes rapid rate of fragmentation underlying the two landforms e.g. Jha et al. (2005) and McGarigal (2006). Woodland habitat displays a patchy type of deforestation, shown by an increased patch number between 1975 and 2012. The slight decline in patch number can be attributed to the strong traditional leadership forest maintenance authority in the 1970s, a responsibility that has now been taken over by the Tanzanian Government that permits logging and farm allocations. Dynamics in mean patch area were observed in the woodland and less dense forest. Notable was the gradual decrease in patch size, while patch number increased by 412 and 391 in dense forest and woodland respectively, an indication of fragmentation patterns in the area earlier observed by Jha et al. (2005). On the other hand, patch area was ideal in characterizing distinct areas with analogous environmental conditions, where patch boundaries are distinguished by discontinuities in environmental character states relevant to the organism or ecological phenomenon under consideration. A combination of patch density (PD), PARA and mean nearest neighbor distance are considered

profound in estimation of the extent of fragmentation in each of the habitats analyzed (Jha et al. 2005). Patch density and PARA are regarded as important in fragmentation assessments, particularly in natural ecosystems because they have a strong influence on ecosystem functioning and ecological processes (McGarigal 2006).

Similarly, a distinct variation in patch number was observed. Woodland and less dense forest had the highest patch number across the years. This can be attributed to the great extent of fragmentation resulting from natural resource exploitation. Furthermore, their vicinity to Morogoro town and management by local authorities may be possible drivers increasing their susceptibility to fragmentation (Fahrig 2001, Fahrig 2003, Wiens 1995, McGarigal 2006, Fischer and Lindenmayer 2007). The woodland habitat had a relatively greater patch density, signifying higher spatial heterogeneity. In addition, the largest patch index was associated with less dense forest while least values were associated with the grassland habitat. This provided information on least and most fragmented landscapes, a good indicator of minimum area requirements for species survival (McGarigal 2006). In addition, the largest patch index, another good indicator for species survival was significant in the less dense forest compared to the rest of the habitats (Rutledge 2003).

Dense forest and woodland had the greater edge density. This could be attributed to increased exposure to farmlands and settlements prevalent in the area. Edge effects characterize the biophysical state of ecosystems at the periphery or in the neighborhood. This is because increased habitat fragmentation exposes habitat to edge effects, compromising the ability of an ecosystem to provide relevant goods and services (Murcia 1995). This limits a habitat's long-term ability to sustain a population as it intensifies species mortality rate (Fahrig 2003). It also influences occurrence of native species populations (Murcia 1995) and ensures that the interaction of species in disturbed environments remains restricted, advancing their mortality risk (Rutledge 2003). Related literature also found a high intensity of fragmentation associated with more edge effects through exposure of contiguous habitats to solar radiation and soil moisture to drier heat conditions (Rutledge 2003).

Games-Howell test results showed a significant level in the perimeter area relationship ($p \leq 0.05$). This could be explained by the fact that less dense forest adjoins dense forest, taking up regions dominated by woodland. It is also possible that the on-going fragmentation is a major driver of conversion of dense forest and woodland to less dense forest. Potential socio-economic drivers could be a result of the expanding Morogoro town and increasing agricultural fields in the adjacent local regions. Similarly, other studies showed how adjoining activities influence intact habitat ecosystems as a result of their structural configuration (Echeverría et al. 2007).

Drivers to habitat fragmentation and conservation implications

Anthropogenic activities significantly influence habitat fragmentation in the region. For instance, extensive farming and urban growth are possible drivers to habitat modi-

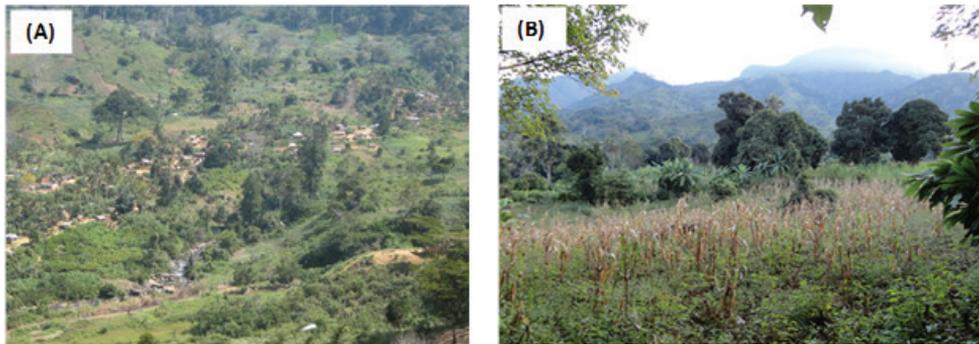


Figure 5. Drivers to fragmentation, note the settlements in the valley and cleared forest in the background and fore ground for crop farming and grazing, respectively (A) and small scale maize and banana fields within the forest in (B).

fication and fragmentation. The area has a conducive montane climate that supports subsistence farming, a prevalent socio-economic activity in the region (Burgess et al. 2007, Swetnam et al. 2011, Yanda and Shishira 1999). This seems to significantly influence all the four habitats. Increasing population growth and consequent increase in settlement and farmlands may have extirpated important fauna and flora in the Ulugurus (Bjørndalen 1992, Burgess et al. 2002, Burgess et al. 2001, Burgess et al. 2007, Swetnam et al. 2011, Hall 2009, Yanda and Shishira 1999) – Figure 5. Habitat fragmentation in the study area can also be attributed to a complex nexus of socio-economic processes (Kessy et al. 2016, Rosales 2008). These processes act at various scales i.e. international (global forest products market growth, commercialization and urbanization), national (changing population, growing local markets and national legislation and governance) and local conditions (livelihoods and levels of poverty) (Wehkamp et al. 2015, FAO 2007, Daly and Farley 2004, Czech 2013). Kessy et al. (2016) for instance notes that local and international demand for timber and agricultural commodities in a globalizing world are major drivers to forest fragmentation in the area. Globalization, with its characteristic scramble by the developing countries to increase their market share on the global marketplace has increased pressure on existing forests and forest land (Hecht and Saatchi 2007, Rosales 2008).

To forestall some of the problems earlier highlighted, the study area, identified as biodiversity hotspots with important ecological functions such as groundwater recharge, surface flow and animal habitat need to be protected from the impacts of land modification and fragmentation. Implications of habitat modification and fragmentation in Morogoro region can be better deciphered through the impact on habitat structure and species losses. The increased habitat losses, mainly attributed to anthropogenic factors may negatively influence genetic diversity and lead to losses of potentially useful genes originally accommodated in intact areas (Ojoyi et al. 2015, Burgess et al. 2007, Swetnam et al. 2011, Hall 2009, Yanda and Shishira 1999, Shirima et al. 2011). Therefore, we recommend that mitigation measures should be adopted to ensure pro-

tection and management of these fragmenting habitat ecosystems. To optimize mitigation measures, the adverse effects of habitat modification and fragmentation need to be understood by all stakeholders. In addition, policy measures and sustainable bottom-up approaches to management and conservation of forest resources should be instituted in the region.

Conclusions

Distinct differences in magnitude of fragmentation were evident across the four habitat categories. The study findings show that fragmentation was highest in less dense forest. Subsistence farming, increasing human population and urban growth are thought to be key drivers to habitat modification and fragmentation, hence it is concluded that anthropogenic processes are the major drivers to habitat fragmentation in the area. The fragmenting landscape is expected to significantly influence floral and faunal vulnerability, likely to compromise the area's ability to among others assimilate organic carbon and to supply socio-economic and environmental goods and services. It is therefore necessary that the study area, and indeed the entire eastern arc mountains region be protected from the impacts of land modification and fragmentation. The study further underscores the value of satellite imagery in concert with relevant reference data in understanding spatio-temporal transformation of vulnerable landscapes arising from anthropogenic processes.

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Effects of forest fragmentation on the morphological and genetic structure of a dispersal-limited, endangered bird species

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Abstract

Throughout the tropics, pristine forests disappear at an alarming pace. This presents a severe threat to forest-dependent species. Especially dispersal-limited understory birds are affected by forest loss. We here explored the effects of habitat fragmentation on the genetic structure and the morphology of the Ecuadorian Tapaculo (*Scytalopus robbinsi*). This bird occurs only in a small range in the premontane cloud forests of southwestern Ecuador. The global population size is declining rapidly due to habitat loss and is currently estimated at only 3000 mature individuals. We caught a total of 28 Ecuadorian Tapaculos in forests of varying size in an area of about 40 km². From each bird, we took morphological measurements and a blood sample. This was used to develop a set of 10 species-specific microsatellite primers for genetic analysis and we found that the Ecuadorian Tapaculos display high levels of genetic diversity. Additionally, we identified dispersal corridors for the species across the landscape using a least-cost path analysis. Notably, we found that wing shape is related to forest size. Individuals in smaller fragments show adaptations of the wing morphology to enhanced mobility and better flight capacity. Our results suggest that the Ecuadorian Tapaculo may rapidly adapt its morphology to the level of habitat fragmentation. This potential can possibly mitigate the risk of local extinctions of the species due to human-caused forest loss and fragmentation.

Keywords

El Oro Tapaculo, cloud forest, habitat fragmentation, wing morphology, genetic diversity, microsatellites

Introduction

Forest loss and fragmentation are among the main drivers of species extinction in the Neotropics. For many forest-dependent species, the amount of available habitat as well as the connectivity between remaining forested patches decline. The sensitivity of a species to forest loss and fragmentation is related to the species' functional traits (Vetter et al. 2011). Especially understory insectivorous birds are sensitive to the logging of forests and therefore particularly threatened by extinction (Stratford and Stouffer 1999, Ferraz et al. 2003, Sodhi et al. 2004). Many of these species have rudimentary dispersal abilities (Moore et al. 2008) and only reluctantly cross large gaps between forest fragments (Sieving et al. 1996, Vergara and Simonetti 2006, Van Houtan et al. 2007). Even smaller distances due to valleys (Krabbe 2008) or roads (Laurance et al. 2004) can contribute to habitat fragmentation for understory birds. Migration is costly for dispersal-limited species, with the costs depending on the distance to be crossed and the mobility of the species (Tischendorf and Fahrig 2000, Moilanen and Hanski 2001). While it is assumed that the population sizes of understory birds shrink due to forest loss, habitat fragmentation makes migration between disconnected populations increasingly difficult for a high number of species.

Small populations are inherently vulnerable to genetic drift and loss of genetic diversity, which constitutes an extinction risk for populations (Frankham et al. 2002). Moreover, reduced connectivity between populations diminishes migration rates and gene flow between them (Epps et al. 2005, Coulon et al. 2006, Segelbacher et al. 2010). In case that disconnected populations are occupying different ecological environments, they may be subject to different natural selection regimes, leading to adaptive divergence of functional traits and population diversity (Hendry and Taylor 2004, Räsänen and Hendry 2008). However, the effects of gene flow and adaptive divergence as drivers of diversification in different environments are controversial (Räsänen and Hendry 2008): First, reduced gene flow may promote adaptive divergence, as it increases the independence of gene pools and the potential to diversify due to different ecological selection regimes (Langerhans et al. 2003, Hendry and Taylor 2004). Second, adaptive divergence can reduce gene flow by the evolution of reproductive isolation (Saint-Laurent et al. 2003, de León et al. 2010). Third, ongoing gene flow can favor adaptive divergence by maintaining genetic variation and non-random dispersal (Garant et al. 2005, Postma and van Noordwijk 2005). Altogether, forest fragmentation can affect the genotype by altering the levels of genetic diversity and gene flow, but can also affect the phenotype by promoting adaptive divergence in case of diverging natural selection.

Insectivorous, forest-dependent birds are particularly sensitive to the fragmentation of forests (Duncan and Blackburn 2004, Sodhi et al. 2004, Vetter et al. 2011). Heavily fragmented habitats can produce significant genetic population structuring already at a small spatial scale of less than 40 km (Moore et al. 2005, Woltmann et al. 2012). Moreover, several studies have reported changes in morphology according to the degree of fragmentation in the distribution range of a particular bird species

(Anciães and Marini 2000, Lens and van Dongen 2000, Desrochers 2010). In less fragmented forests, birds are likely to develop shorter, rounder wings than in heavily fragmented habitat, which proved advantageous for maneuvering in dense vegetation (Desrochers 2010). Longer, pointed wings enhance mobility in heavily disturbed and fragmented forests (Fiedler 2005, Desrochers 2010).

In this study, we examined the effects of forest fragmentation on the genetic and morphological structure of the Ecuadorian Tapaculo (*Scytalopus robbinsi*, Rhinocryptidae), a species almost unknown to science. This bird is endemic to the understory of cloud forests in southwestern Ecuador. In general, Tapaculos are among the species most sensitive to habitat fragmentation and are therefore considered an ideal model for assessing fragmentation effects on dispersal-limited species (Castellón and Sieving 2006). Throughout the distribution range of the Ecuadorian Tapaculo, forests are heavily degraded and fragmented, affecting the habitat of not only Tapaculos, but also of other dispersal-limited, understory species like antbirds, antpittas or hummingbirds. It is estimated that over 90% of the original forest cover in southwestern Ecuador has been logged since the beginning of the 20th century (Dodson and Gentry 1991, Best and Kessler 1995). From 2005 to 2010, the deforestation rate in Ecuador was 1.89%, which is the highest rate in South America (FAO 2010). The population size of the Ecuadorian Tapaculo thus is assumed to be declining rapidly (Krabbe and Schulenberg 1997, Hermes et al. in press) and likely the remaining populations are strongly isolated from each other, with ongoing deforestation disrupting linkages between them. The Ecuadorian Tapaculo has only limited dispersal abilities and avoids crossing areas of un-forested habitat (Krabbe and Schulenberg 1997, Hermes et al. in press). Therefore, it is possible that migration rates between different populations confined to disjunctive forest fragments are low, resulting in a clear fine-scale genetic structure, as it was shown for a similar understory bird species (Woltmann et al. 2012). In view of the high level of forest loss throughout the distribution range of the Ecuadorian Tapaculo, it is possible that individuals show morphological differences depending on the degree of fragmentation. Morphological adaptations of the flight apparatus in relation to the level of habitat fragmentation could mitigate negative effects of forest loss by improving the dispersal abilities of Ecuadorian Tapaculos and thereby maintaining population connectivity.

The ability of a species to cope with ongoing habitat fragmentation can determine its abilities to persist in a changing environment and avoid local extinction (Castellón and Sieving 2006, Stouffer et al. 2006). Therefore, we want to investigate the effects of forest fragmentation on the morphology of the Ecuadorian Tapaculo, on the level of genetic diversity and on gene flow between populations. Detailed information about these effects are crucial to make scientifically sound recommendations for conservation measures not only for this endemic species, but also for other forest specialists restricted to this kind of habitat. Given the presumably low dispersal abilities of the species and, at the same time, the high level of habitat fragmentation in the study area, we expect migration rates and gene flow between forest patches to be reduced, leading to genetically distinct sub-populations. However, not only is the species' ecology unknown, but also genetic information is lacking. We thus caught individuals to assess

the genetic status of the population. We expected to find genetic differentiation between individuals caught in locations separated by dispersal barriers, like areas of open habitat, unsuitable elevation, or highways. To identify corridors with low dispersal cost, i.e., the optimal routes for migration of Ecuadorian Tapaculos, we calculated least-cost paths between territories. Moreover, we assessed morphological differences of birds caught in different sites of the study area; we predicted to find differences according to the level of habitat fragmentation.

Methods

Study species and study area

The Ecuadorian Tapaculo, also known as El Oro Tapaculo, is an insectivorous bird endemic to a small range (~ 1100 km²) on the western slopes of the Andes in southwestern Ecuador, at an elevation of 850–1500 m (Hermes et al. in press). The species was only discovered in 1990 (Krabbe and Schulenberg 1997) and is so far not well studied. It occurs in the undergrowth of mature forests and is very reluctant to cross even small areas of open habitat (Krabbe and Schulenberg 1997). Being practically unable to fly longer distances, Tapaculos move around by hopping or walking (Reid et al. 2004, Castellón and Sieving 2006). The IUCN classifies the Ecuadorian Tapaculo as endangered. Global population size is estimated to range between 1900 and 4600 mature individuals (Hermes et al. in press). It is feared that the species' requirements for high-quality habitat and presumed susceptibility to forest degradation and fragmentation have led to a severe population decline, which might still be ongoing (Hermes et al. in press).

The only protected site within the range of the Ecuadorian Tapaculo is the private Buenaventura reserve in the canton Piñas (3.655°S, 79.744°W), established in 1999 by the Ecuadorian NGO Fundación Jocotoco. This reserve covers an area of 2300 ha in an elevation of 400–1500 m (Figure 1). The predominant vegetation types within the reserve are secondary forests in various successional stages, which are separated by areas of abandoned pasture. Outside the reserve, deforestation is intense, with mostly only forest patches smaller than 100 ha remaining. The main causes for the logging of forests are intensification of agriculture and forest clearance for livestock. Natural forests mainly persist in areas which are not suitable for conversion into cattle pasture or cropland, like steep slopes or river banks (Best and Kessler 1995).

Field work was carried out between December 2013 and May 2014 and between November 2014 and January 2015 in the Buenaventura reserve, and near Ñalacapa, about 5 km south of Buenaventura (Figure 1). The study area is located at the southern end of the Ecuadorian Tapaculo's distribution range, covering about 5% of the total range. The size of forest fragments was assessed in ARCMAP 10.2 using satellite images of the area as a template (Hermes et al. in press). Forest areas ranged from about 15 ha to 900 ha. The northern and southern part of the study area was divided by a highway and a valley with an altitude of about 400 m.

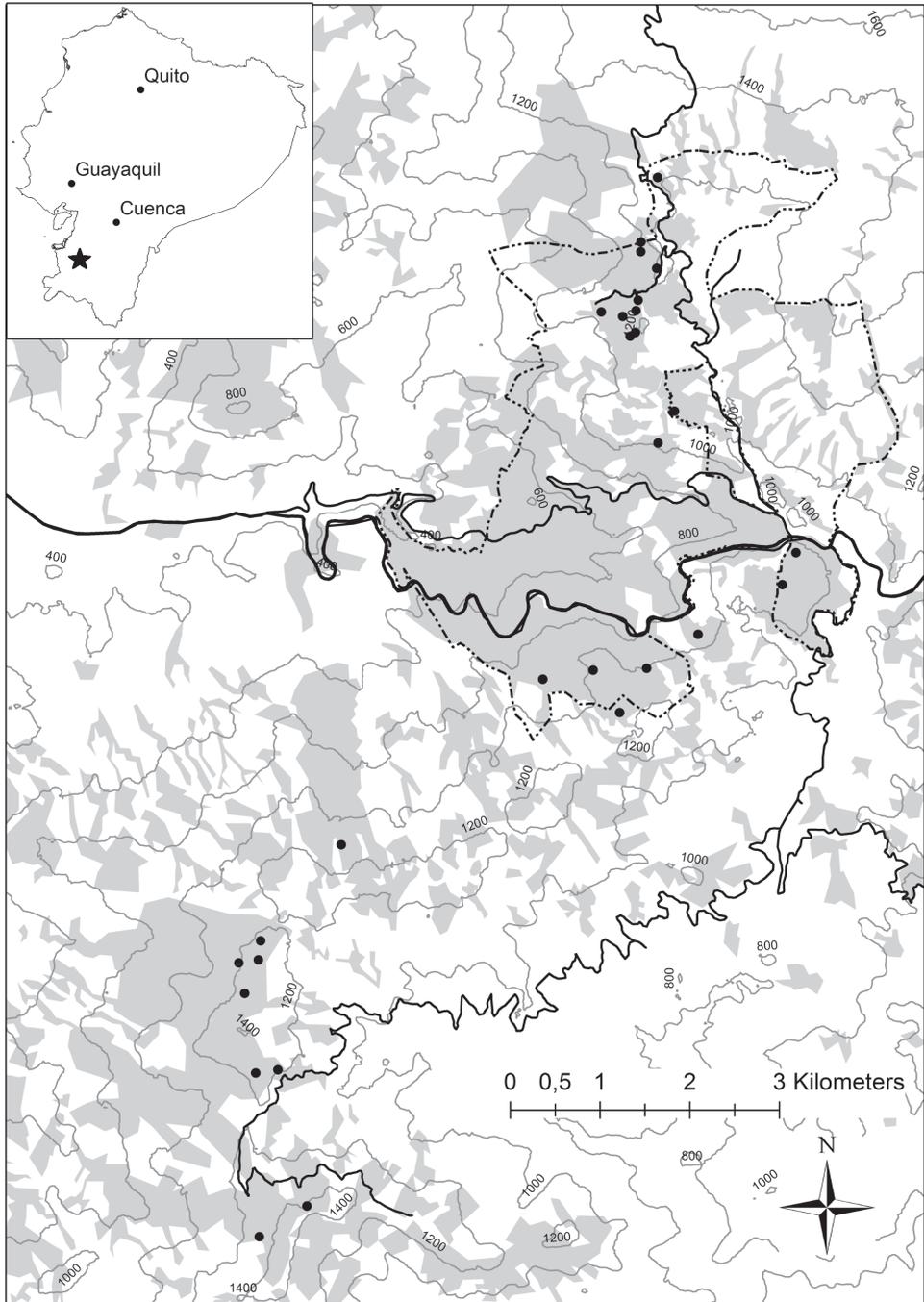


Figure 1. Map of the study area in southwestern Ecuador. Forested areas are shaded grey, whereas white areas represent non-forested areas (mainly cow pastures). The Buenaventura reserve is circled by the dashed line. The bolt black line represents a highway cutting the reserve into a northern and a southern part, while minor roads are indicated by the thin lines.

Bird sampling

For bird capturing, we used mist-nets and tape recordings of the song of male Ecuadorian Tapaculos as a decoy. If an individual approached the playback, observers herded it into the net. The Ecuadorian Tapaculo's secretive behavior, very good vision and excellent maneuverability made the capturing very challenging. We captured 28 males. Birds were ringed with a standard aluminum ring and color-banded individually. Then, individuals were weighed and the lengths of tail, tarsus, wing, primary feathers and the first secondary feather were measured. From each individual, we took a blood sample from the brachial vein. To minimize stress, birds were handled within less than 10 minutes of capture and released unharmed to the same sites. Blood samples were stored in 99.8% ethanol and transferred into a -20 °C freezer.

Assessment of morphological differences

To obtain an index for body size, we carried out a principal component analysis (PCA) for all the morphological variables that we recorded. As variables differed in their numerical range, they were z-standardized prior to the analysis. A second PCA for the variables wing length and length of the feathers P9 to S1 provided an index for the wing shape. For both PCAs, missing values (e.g., caused by feather molt) were replaced by the mean. Additionally, we quantified the body condition of each individual using the scaled mass index (Peig and Green 2009). Then, we tested for relationships between an individual's morphology and the size of the forest where it was captured. To this aim, we carried out Kendall correlations between the fragment area and the first principal components of the PCAs for body size and wing shape as well as the body condition index. The statistical analysis was carried out in R 3.3.0 (R Development Core Team).

Analysis of genetic population structure

We extracted DNA from the blood samples and compiled a set of 10 species-specific microsatellite primers (for a description of the primer development see Supplementary File). Two individuals had to be excluded from the analysis due to failure of amplification during PCR in two loci. Then, we applied a Bayesian clustering method using the program STRUCTURE 2.3.4 (Pritchard et al. 2000) to explore the genetic population structure of the individuals ($n = 26$) caught in different fragments. This program uses a Markov chain Monte-Carlo (MCMC) approach to compute the probability of the sampled individuals belonging to a given number K of discrete genetic subpopulations. An admixture model with correlated allele frequencies was used. We pre-defined the parts north and south of the highway as distinct sampling locations (Figure 1).

We set K from 1 to 8 and carried out 10 runs for each K , with 10^6 MCMC iterations and 500,000 burn-in iterations for each run. We determined the best value for K by analyzing the probability scores in the program STRUCTURE HARVESTER (Earl and vonHoldt 2012).

Least-cost paths and isolation by distance

Landscape barriers disrupting or decreasing connectivity between individuals or populations can be quantified and qualified by the creation of a resistance map, which allocates a specific resistance value to each cell of the land cover grid according to the mobility of the species (Adriaensen et al. 2003). To evaluate landscape permeability for Ecuadorian Tapaculos in the study area and to assess least-cost paths (LCPs) between the individuals, we created a resistance map accounting for species-specific demands and landscape features. We produced a map (cell size 30 x 30 m) for the parameters 'forest cover', 'elevation', and 'roads' by assigning them different weights in the RASTER CALCULATOR tool of ARCMAP. Weights were determined on expert-opinion based on literature review and observations of the behavior of individuals. As Ecuadorian Tapaculos are reluctant to cross open habitats without forests (Krabbe and Schulenberg 1997), we assumed the costs for crossing open areas to be 100-fold higher than for dispersing through forests. Roads are known to represent a strong dispersal barrier for understory birds; even narrow, unpaved roads significantly reduce dispersal, while highways can even entirely block movement (Laurance et al. 2004). We created a buffer zone with a radius of 15 m around the roads in the study area in order to obtain a continuous reproduction of the roads on the 30 x 30 m resolution of the map. We assigned a 200-fold weight to the highway dissecting the northern and southern part of the study area, while the less frequented country lanes only obtained a 100-fold weight. For the resistance values of the elevation, we considered the mean altitude of territories to be the optimum for Ecuadorian Tapaculo, with dispersal costs being zero. There are hints that the Ecuadorian Tapaculo is sensitive to elevation. Presumably, the species has shifted its distribution range uphill within the last decades and now avoids areas of lower elevation (Hermes et al. in press). Therefore, higher or lower elevations were assigned costs equaling the difference in altitude to the mean altitude of territories. Merging of the layers generated the resistance map. The LINKAGE MAPPER tool of ARCMAP was then used to identify the LCP between territories by detecting cells with the lowest costs while avoiding cost-intensive cells.

To assess isolation by distance, we tested for relationships between the genetic and the geographic distances between the individuals. Geographic distance was expressed by Euclidian distance between territories as well as by LCP length and LCP cost. In GENALEX 6.5 (Peakall and Smouse 2012), we carried out Mantel tests with 999 permutations for each of the three parameters separately.

Analysis of past genetic diversity and population size change

Using the R package HIERFSTAT, we tested whether genetic diversity has been reduced since the species was discovered in 1990. Accounting for the difference in sample size between the two groups, we compared allelic richness of the 26 samples we took in 2013–2015 with those of seven museum specimen collected in 1990–1991 in the same area (from the tissue collection at the Zoological Museum Copenhagen; sample numbers 125057, 125070, 125071, 125072, 126057, 126058 and 126167).

Additionally, we tested for a potential decline in the effective population size in the past with the program MSVAR 1.3 (Beaumont 1999, Storz and Beaumont 2002). This program was shown to be particularly powerful at detecting severe and ancient population declines (Girod et al. 2011), and can deal with small sample and population sizes (Beaumont 1999). Using multilocus microsatellite data, MSVAR applies a Bayesian coalescent-based hierarchical model to estimate the current population size as well as the ancestral population size, the time since a potential population decline or expansion started and the mutation rate of loci. With MCMC simulations, the program quantifies the likelihood of observing the allele frequencies in a sample, given a pre-defined demographic and mutational model. The simulation then produces probability estimates for the above-mentioned parameters by maximizing the likelihood of the observed data. We ran the model four times. To avoid a bias on the posterior distribution, each time we used different prior information assuming different scenarios of past population size change. We ran each chain with 10^9 iterations and a thinning interval of 100,000. Thus, we obtained an output of 20,000 iterations for each run and dismissed the first 5,000 iterations as burn-in. The output was analyzed using the R packages CODA, BOA and LOCFIT. We checked the output chains for convergence using the Gelman-Rubin analysis (Gelman and Hill 2007) and calculated modes and 95% highest probability density (HPD) intervals for each parameter. Parts of the R script were taken from Paz-Vinas et al. 2013.

Results

Bird morphology in relation to forest size

The first four principal components (PCs) of the PCA of body size accounted for 71.92% of the variance of 14 morphological variables (Table 1). We assigned loadings above a threshold of 0.35 to the respective PC. PC 1 described the length of the inner primary feathers P5, P3, P2 and P1, while PC 2 described the outer primary feathers P9, P8 and P7. PC 3 characterized the length of tarsus and the P4 feather, and PC 4 described the length of wing and tail. The PCA for the wing shape yielded similar results, with the first three PCs accounting for a total of 74.82% of the variance (Table 2). Here, PC 1 also represented the primary feathers P5, P3, P2 and P1. PC 2, accordingly, described the feathers P9, P8 and P7. PC 3 characterized the total

Table 1. Body size of Ecuadorian Tapaculos. Principal component analysis for the body size of 28 Ecuadorian Tapaculos, with the loadings, eigenvalues and variance of the first four principal components (threshold: 0.35; bold font).

Variables	Loadings			
	PC 1	PC 2	PC 3	PC 4
Tarsus	-0.037	-0.052	0.641	0.087
Wing	-0.170	0.001	-0.326	0.549
P9 feather	-0.187	-0.534	-0.185	-0.173
P8 feather	-0.269	-0.398	-0.024	-0.045
P7 feather	-0.270	-0.356	0.102	-0.190
P6 feather	-0.321	-0.258	-0.077	0.029
P5 feather	-0.356	0.102	-0.180	0.327
P4 feather	-0.203	0.193	-0.355	-0.193
P3 feather	-0.388	0.202	0.041	-0.003
P2 feather	-0.373	0.238	0.041	0.067
P1 feather	-0.371	0.189	0.240	-0.069
S1 feather	-0.300	0.235	0.317	-0.192
Weight	0.002	-0.339	0.267	0.174
Tail	0.043	-0.095	0.205	0.634
Eigenvalue	5.202	1.889	1.627	1.351
Variance explained	37.16%	13.49%	11.62%	9.65%

Table 2. Wing shape of Ecuadorian Tapaculos. Principal component analysis for the wing shape of 28 Ecuadorian Tapaculos, with the loadings, eigenvalues and variance of the first three principal components (threshold: 0.35; bold font).

Variables	Loadings		
	PC 1	PC 2	PC 3
Wing	-0.174	0.004	0.669
P9 feather	-0.187	-0.593	0.050
P8 feather	-0.270	-0.401	-0.047
P7 feather	-0.270	-0.363	-0.346
P6 feather	-0.323	-0.292	0.042
P5 feather	-0.359	0.106	0.379
P4 feather	-0.205	0.126	0.167
P3 feather	-0.388	0.207	-0.050
P2 feather	-0.372	0.261	0.082
P1 feather	-0.359	0.230	-0.224
S1 feather	-0.300	0.284	-0.442
Eigenvalue	5.188	1.787	1.256
Variance explained	47.16%	16.25%	11.42%

wing length, as well as the length of the feathers P5 and S1. We concluded that, for both PCAs, individuals with high values for PC 1 have shorter inner primaries, i.e., a narrow wing, and individuals with high values for PC 2 have shorter outer primaries, i.e., a less pointed wing.

For both PCAs, we detected a marginally significant relationship between PC 1 and forest size (PCA of body size: $P = 0.057$; $\tau = -0.273$; and PCA of wing shape: $P = 0.063$; $\tau = -0.267$; Kendall correlation). None of the other PCs correlated with forest size (all $P > 0.12$; Kendall correlation). Similarly, there was no relationship between the body condition of birds and the size of the forest fragments ($P = 0.76$; $\tau = 0.044$; Kendall correlation).

Genetic diversity, population genetic structure and gene flow

Allelic richness of the museum samples was 3.80 ± 0.75 , while that of the recently collected samples was 3.59 ± 0.57 . Therefore we concluded that genetic diversity has not changed within the last ~ 25 years. The STRUCTURE analysis showed no clear population substructure. $K = 1$ yielded the highest probability, indicating that most likely all samples belonged to the same population. However, error bars were highly overlapping amongst the estimates for different numbers of clusters (Figure 2).

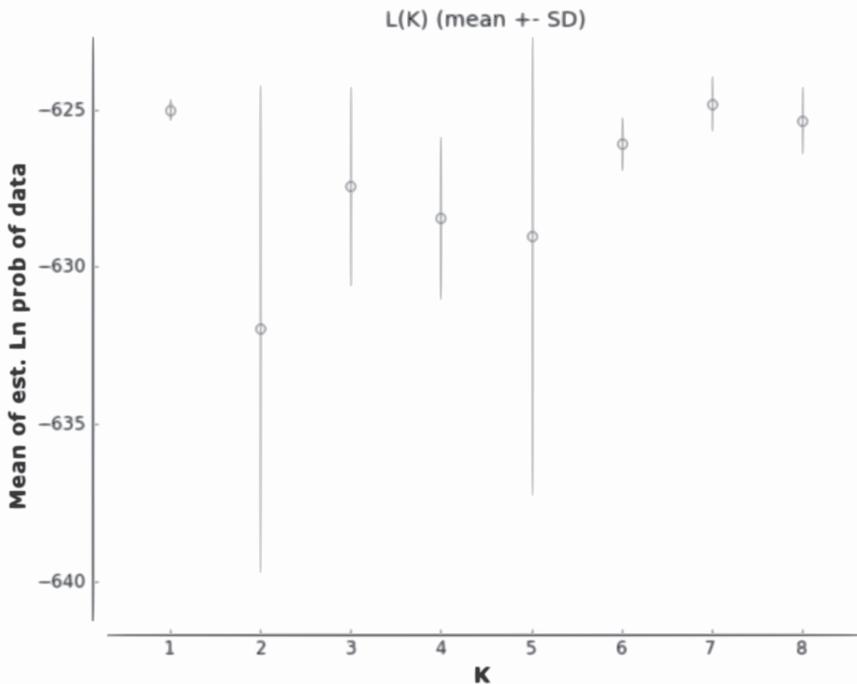


Figure 2. Mean \pm SD of the log-likelihood for $K = 1$ to 8 distinct genetic populations. Strong support for $K = 1$ indicates that most likely all the samples stem from the same genetic group.

With the least-cost path analysis, we could identify a dispersal corridor for Ecuadorian Tapaculos across the study area, which circumvented the valley between the northern and southern part (Figure 3). Mantel tests indicated clear evidence for isolation by distance. Euclidian distance showed the strongest relationship to the genetic distance ($R_{xy} = 0.418$; $P = 0.001$), followed by LCP length ($R_{xy} = 0.399$; $P = 0.001$) and LCP cost ($R_{xy} = 0.319$; $P = 0.001$).

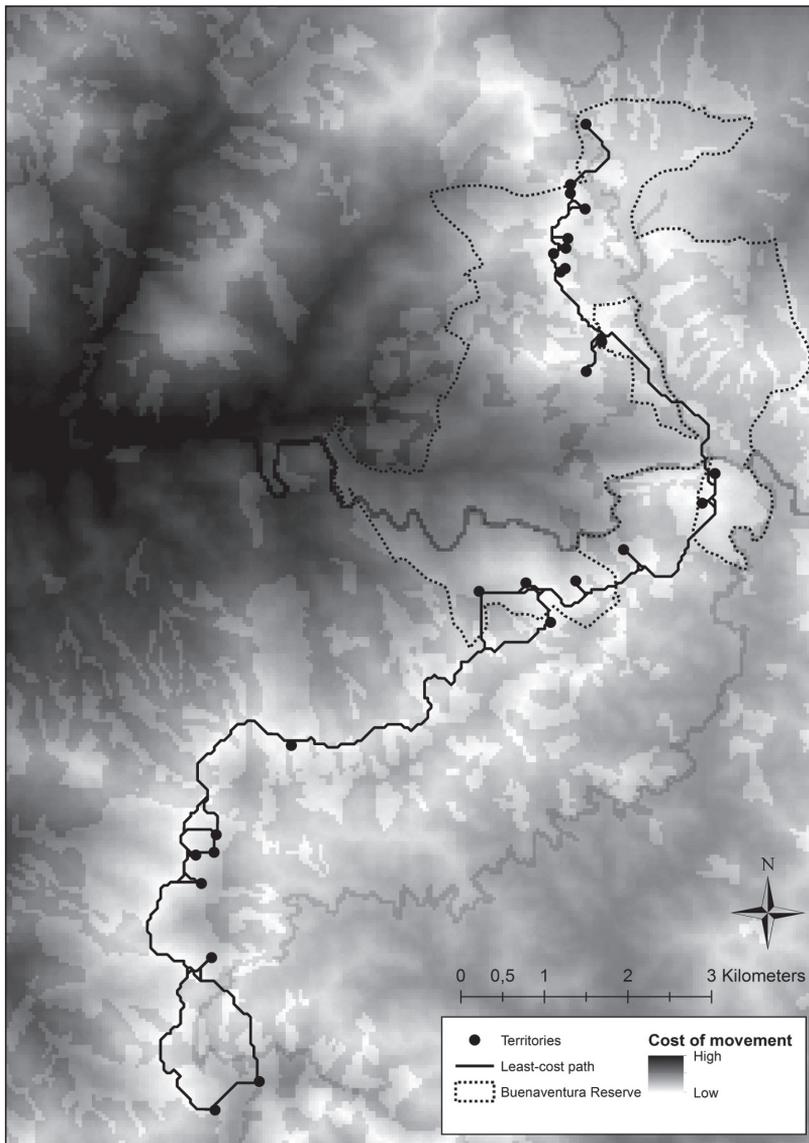


Figure 3. Resistance map with least-cost path. The cost of movement is visualized by the color gradient from black to white, with black indicating higher costs and white lower costs. The bolt black lines show the least-cost paths between 26 Ecuadorian Tapaculo territories in the study area.

Past demographic changes

Modelling the population demography yielded evidence of a severe population decline in the past. All potential scale reduction factors were < 1.1 , so we concluded that chains converged well (Gelman and Hill 2007). Modal values (and 95% HPD intervals) indicated a current effective population size of 770 individuals (150–2,820). Ancestral population size was 26,000 (5,275–171,400), suggesting an approximately 30-fold population decline. Time since the population started decreasing was estimated to about 7000 years (870–52,000) and the mutation rate to $1.42e^{-4}$ ($1.32e^{-6}$ – $7.23e^{-3}$). However, the large probability density intervals for the parameter estimates indicate a high level of uncertainty in the simulation.

Discussion

In this study, we investigated the genetic and morphological structure of the Ecuadorian Tapaculo, an endangered bird endemic to the understory of premontane cloud forests in southwestern Ecuador. In the study population, genetic diversity has remained constant within the last 25 years, even though the global population has declined dramatically. Despite the fact that forests are highly fragmented and the species has only limited dispersal abilities, we did not detect a structuring into genetically distinct sub-populations on a scale of 40 km². Notably forest size influenced bird morphology, with individuals in larger fragments having rounder wings than their conspecifics in smaller forests.

Population genetics of the Ecuadorian Tapaculo

Throughout the study area, we found no genetic structuring among Ecuadorian Tapaculos, indicating that a substantial amount of gene flow is still maintained. Even though the Ecuadorian Tapaculo is a bad disperser, migration between different forest fragments seems not to be blocked. We expected that habitat fragmentation in the range of the species produced genetically distinct populations in different forest fragments, as it was shown for a similar species (Woltmann et al. 2012). Our study area was disrupted by a valley and a highway, which we expected to act as barriers to dispersal. Besides, the distances between the different forest fragments following the least-cost path ranged between 10 m and 400 m and were thus partly larger than the mean dispersal distances observed for Ecuadorian Tapaculos (80 m; Hermes et al. in press). Nevertheless, we did not detect genetic structuring in distinct sub-populations. Similarly, a study analyzing genetic differentiation in White-ruffed Manakins (*Corapipo altera*) at a comparable scale than our study did not detect genetic structuring either, although the habitat was highly fragmented (Barnett et al. 2008). However, fragmentation does not necessarily lead to reduced gene flow and genetic differentiation (Galbusera et al. 2004). Even a species with strong dispersal limitation can show low levels of differentiation across a

highly fragmented landscape (Callens et al. 2011). In the case of the Ecuadorian Tapaculo, even the high degree of forest fragmentation in the northern part of the study area is not sufficient to cause genetic structuring.

Gene flow across the study area is not impeded by barriers and Mantel-tests between genetic and geographic distances suggest isolation by distance (IBD). In theory, IBD can lead to considerable genetic differentiation even at small scales (Wright 1943). In the most extreme dispersal event observed in the Ecuadorian Tapaculo, an individual crossed 245 m of un-forested habitat to establish a territory in a remote forest fragment (Hermes et al. in press). The IBD detected here is therefore likely a consequence of the generally low dispersal capacities and mean migration distances of the species, which are reinforced by forest fragmentation.

Genetic diversity of Ecuadorian Tapaculos in the study area remained constant between 1990 and 2015. On a global scale however, population size and most likely also genetic diversity still decrease. Even though the result of the analysis of past population demography yielded a high level of uncertainty and should therefore be treated with caution, it gave evidence of a severe population decline. The Buenaventura reserve remains until now the only protected site within the distribution range of the Ecuadorian Tapaculo. Around the reserve, forests are heavily fragmented and degraded; mostly, patches are smaller than 100 ha and consist of young secondary stands. The constant level of genetic diversity in the study population over 25 years, which is presumably attributable to the establishment of the reserve, shows that a negative population trend can be stopped. However, in order to achieve a change for the better on the scale of the global population of Ecuadorian Tapaculos, it would be necessary to protect remaining forests throughout the entire distribution range, which, in view of ongoing deforestation, seems implausible. In general, Tapaculos are among the understory species most sensitive to fragmentation and are therefore seen as umbrella species for conservation planning (Willson et al. 1994, Reid et al. 2002, Castellón and Sieving 2007). The fact that we found population connectivity and a constant high level of genetic diversity in the Ecuadorian Tapaculo gives hope that other understory birds and dispersal-limited mammals in the area show similar population trends.

Morphological adaptations to forest fragmentation

While several studies have already addressed the effects of forest fragmentation on the genetic structure of a population, its effects on individual morphology are far less examined. However, the degree of habitat fragmentation can cause different morphological adaptations in birds (Desrochers 2010). Increasing distance between forest fragments exerts a selective pressure for enhanced mobility and flight ability, i.e., more pointed wings, in order to enable migration between remote fragments (Fahrig 2003, Fiedler 2005, Desrochers 2010). While the studies of Fiedler (2005) and Desrochers (2010) were carried out at a much larger spatial scale (several 1000 km), we found effects on wing morphology already at a distance of less than 15 km.

Ecuadorian Tapaculos have short, round wings and only limited flight capacities; they do rarely fly distances longer than 3 m and move mainly by walking or hopping (Krabbe and Schulenberg 1997). In this study, we found wing shape to be related to forest size. Individuals in small patches had narrow wings, which can be seen as an adaptation to enhanced mobility and better flight capacity, which probably allowed colonization in the first place. In larger fragments, on the other hand, selection pressure for increased mobility is absent. Dispersing individuals do not face the necessity to cross habitat gaps before establishing their territories. For movement within large fragments, round wings enabling good maneuverability are advantageous. Alternatively, the differences in wing shape could be caused by different structural characteristics of the understory layer in relation to fragment size, with pointier wings facilitating flights in search for food. However, microhabitat structure of the understory in the forest fragments was assessed in a previous study (Hermes et al. in press), but had no influence on wing shape. Therefore, we conclude that the morphological differences are most likely caused by the fragmentation of forests and not by the degradation within forests.

Wing morphology is highly heritable in birds (Boag and van Noordwijk 1987). In this study, we detected effects of forest fragmentation on the morphology of the species already in a small population and at a small spatial scale. This implies that habitat fragmentation exerts considerable selective pressure favoring adaptive divergence of wing morphology. However, the morphological variability of the Ecuadorian Tapaculo gives evidence of the species' potential to rapidly adapt to environmental changes. This potential can possibly mitigate the risk of local extinction of the Ecuadorian Tapaculo due to human-caused forest loss and fragmentation.

In the study population, phenotypic divergence in wing shape could arise in sympatry. Even though the individuals in the study area were not genetically differentiated at neutral markers, the morphological changes are likely promoted by the isolation by distance we discovered over the study area. Moreover, the differences in the level of forest fragmentation likely exert a selective pressure, which is strong enough to produce distinct phenotypes despite the homogenizing effect of gene flow. If the diverging selective pressures are high, a new beneficial allele can fix quickly and affect the genome (Crisci et al. 2016). In the case of the Ecuadorian Tapaculo, morphological adaptations have possibly arisen rapidly after the onset of intense forest fragmentation at the beginning of the 20th century. Similar to our results, a study on Wedge-billed Woodcreepers (*Glyphorhynchus spirurus*) found considerable morphological differences, although the level of gene flow was high (Milá et al. 2009). Generally, gene flow is assumed to constrain adaptive divergence by homogenizing the gene pool (Hendry and Taylor 2004, Räsänen and Hendry 2008). However, adaptive divergence caused by environmental differences can also constrain gene flow by the evolution of reproductive isolation over a few generations, i.e., ecological speciation (Schluter 2000, Carroll et al. 2007, Hendry et al. 2007). Moreover, in case that the adaptive divergence reduces the fitness of migrants between different environments, a negative feedback loop

can be initiated: Reduced fitness of migrants reduces dispersal between the different environments, which in turn reduces gene flow. This can lead to a further increase in adaptive divergence and a further reduction in dispersal and gene flow (Räsänen and Hendry 2008). It is possible that the Ecuadorian Tapaculos are currently beginning a similar loop. Their flight apparatus is adapted to the specific level of habitat fragmentation and can be disadvantageous in different conditions. Therefore, the fitness of birds migrating to forests with a differing degree of fragmentation is likely reduced. Even though gene flow is not diminished at present, it is possible that it will decrease in future under ongoing diverging selection, forming genetically and morphologically distinct sub-populations. Nevertheless, this is not the only possible future scenario. Throughout the study area, considerable reforestation efforts have been made within the last 20 years. Forest regrowth increases habitat availability and homogeneity for the Ecuadorian Tapaculo. Thus, assuming far-reaching reforestation programs, the selective pressure for adaptations to enhanced mobility might disappear, reducing the divergence in wing morphology and increasing gene flow.

Compliance with ethical standards

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Ethical approval: All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All procedures performed in studies involving animals were in accordance with the ethical standards of the institution or practice at which the studies were conducted. Permissions to conduct field work (No. 005-IC-FAN-DPEO-MAE) and to export samples (No. 05-2014-FAU-DPAP-MA) were granted by Ministerio de Ambiente and Ministerio de Agricultura, Ganadería, Acuacultura y Pesca, Ecuador.

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Supplementary material I

Development of species-specific microsatellite primers

Authors: Claudia Hermes, Annika Döpfer, H. Martin Schaefer, Gernot Segelbacher

Data type: Adobe PDF file

Explanation note: The supplementary material contains a detailed description of the development of a set of 10 microsatellite primers for the Ecuadorian Tapaculo, including primer sequences and gene bank accession numbers.

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Informed debate on the use of fire for peatland management means acknowledging the complexity of socio-ecological systems

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Abstract

The effects of fire and its use on European peatlands and heaths are the focus of considerable research and debate due to the important services these ecosystems provide and the threats they face from climatic and land-use change. Whilst in some countries ecologists are actively promoting the restoration of historic fire management regimes, in the UK the debate has become increasingly acrimonious. Positions seem entrenched between continuing the intensive form of management associated with grouse moors or ceasing burning and seeking to eliminate fire altogether. In a recent paper we argued that participants' positions appeared influenced by political and philosophical beliefs associated with, for example, private land-own-

ership, hunting, and associated conservation conflicts such as raptor persecution. We also suggested there was inadequate engagement with key concepts and evidence from fire and peatland ecology. We argued that management debates should aim to be inclusive and evidence-based, and to understand the benefits and costs of different fire regimes. In a strongly-worded critique of our paper, George Monbiot (author of “Feral: Searching for Enchantment on the Frontiers of Rewilding”) suggested we: i) framed our research question too narrowly; ii) made the implicit assumption that moorlands were the “right” ecosystem for the UK countryside; and iii) failed to adequately engage with arguments put forward for cessation of managed burning. Here we critically examine each of these issues to provide further insight into how adaptive, participatory land-management could develop. We argue that a productive debate must acknowledge that complex trade-offs are inevitable during ecological management. Choosing the “right” ecosystem is difficult, especially in a landscape with a long history of human influence, and the answer depends on the values and ecosystem services we prioritize. Natural resource management decisions will be improved if based on an understanding and valuation of the multiple scales and levels of organization at which ecological diversity exists, the role of disturbance in controlling ecosystem composition and function, and the need for participatory action.

Keywords

Adaptive Management, diversity, heathland, managed burning, moorland, participatory, scale

Introduction

The ecological effects of fire in European peatlands and heathlands are the focus of considerable research and debate due to the important services these ecosystems provide (Whitfield et al. 2011), their conservation importance (Thompson et al. 1995), and the threats they face from climatic (Gallego-Sala et al. 2010) and land-use changes (Acs et al. 2010). Though heathland and peatland ecosystems occur naturally in NW Europe, for instance at high elevations above the tree-line or in areas of cool temperatures and high rainfall, across much of their British range heathlands and peatlands are fundamentally anthropogenic landscapes deriving their current ecological composition, structure and function from millennia of low-intensity human management (Simmons 2003). Despite this, human interventions in the more recent past, including drainage, high rates of livestock grazing, and intensive use of managed burning have interacted with other anthropogenic impacts such as nutrient deposition, acidification and climate change to have significant ecological consequences (Holden et al. 2007). Each of these drivers can affect biodiversity and ecosystem services in their own right, but they also vary significantly in time and space and interact with each other in complex ways (e.g. Evans et al. 2014). Fire is a critical control on the current structure and function of peatlands but over time we have grown concerned that the dominant narrative in the UK surrounding the use of fire as a management tool has become antagonistic, politicised and overly-simplified. We are not alone in being concerned about the tone of upland land-management debates in the UK. Wynne-Jones (2016) recently critiqued the hyperbolic character of the debate regarding interactions between upland sheep farming, reforestation and catchment hydrology. The current debate about managed burning risks failing to adequately acknowledge the complexity associated with

multiple drivers of peatland ecosystem function, our growing global understanding of the ecological effects of fire in peatlands (e.g. Turetsky et al. 2015) and the potential flexibility of prescribed burning as a management tool (Russell-Smith and Thornton 2003). We laid out our concerns in a recent paper “The role of fire in UK peatland and moorland management: the need for informed, unbiased debate” (Davies et al. 2016), which has been the subject of subsequent discussion, debate, and no small amount of misrepresentation.

Notable amongst the coverage our paper received was the critique made by the respected author, journalist and commentator George Monbiot (Monbiot 2016a). Monbiot’s comments followed newspaper reports (e.g. Webster 2016) which, without consulting us, reported on our paper before it was published and distorted our key messages. After mistakenly being placed open access on an institutional server following its acceptance, our paper was picked up by the organization “You Forgot the Birds” (YFTB) which produced a press-release based on it. In subsequent newspaper reports (e.g. Webster 2016), Monbiot and the Royal Society for the Protection of Birds (RSPB) were publicly and unfairly criticized, based on a partial reading of our work, highly selective quoting from our paper and a distortion of our conclusions. We made it clear at the time that we did not endorse any of the pre-publication coverage of our paper (Avery 2016). It is deeply ironic that our paper, which called for unbiased, informed science reporting, was used in this way given that we specifically criticized science journalism for failing to adequately engage with the authors of research papers, for not seeking or allowing pre-publication review of their articles, and for a tendency to be insufficiently critical of simplified and sometimes biased press-releases.

Given the wider issues Monbiot (2016a) raised regarding peatland and moorland ecology, we feel it is important to respond to his criticisms and to develop our arguments further. By our reading, Monbiot has three key issues with our paper: i) that we frame our question too narrowly and thus pre-empt our own conclusions to favour the continued use of current forms of burning; ii) that we make the implicit assumption that moorlands are the appropriate ecological state for large areas of the British Uplands; and iii) that we failed to read and/or understand one of his recent articles and, as a result, did not adequately engage with his criticisms of burning or his arguments in favour of “rewilding”. We believe his conclusions stem from not unusual misunderstandings regarding:

1. How scientists frame research questions within the context of peer-reviewed journal publications and why we chose to focus our paper on the ecology of peatland fires.
2. The ecological, social, economic and conservation importance of peatland and heathland ecosystems.
3. The nature of ecological diversity and the importance of considering ecological patterns and processes across multiple scales.

These misunderstandings are important as they potentially influence one’s attitudes regarding the role of science in the development of conservation policy and man-

agement decision-making, how one reads and interprets scientific literature and how one assesses the value of peatland and heathland landscapes and fire's role in them. Our aim here is to address each of the three points above before considering how this knowledge should influence attitudes towards land-management and the character of ecological debates.

I. Framing research questions – understanding fire effects on peatlands

A scientific paper, even a review or opinion piece, aims to shed light on a particular, focused question. Debates regarding ecosystem management and restoration are inherently complex and require an integrated understanding of socio-ecological systems. However, within these larger debates one can still identify specific process and interactions each of which often require detailed study on their own before the whole picture can be constructed (Figure 1). Arguments can often develop at cross-purposes due to misunderstandings regarding the particular element of the system being studied or debated. The objectives of our paper were to i) review recent evidence of the effects of fires (managed and wild) on moorland and blanket bog ecosystems; and ii) examine the manner in which this knowledge is communicated in scientific publications and the media. This focus is rather different from the socio-cultural debates Monbiot (2016a) primarily focused on (Figure 1). We believe our objectives were justified because as we, and others (e.g. Graves et al. 2013), have explained, there is considerable debate about the environmental effects of managed burning and wildfires on peatland ecosystems and ecosystem services. We believe that the debate about environmental processes is being muddied by wider political, social and economic issues, and a highly simplistic view of fire management. This would have us believe that the only options are to cease or ban burning entirely, or to continue with an intensive use of fire as associated with management on some grouse moors (see Figure 1 in Davies et al. 2016a). This is a simplification of the significant variation in current and historic managed and wild fire regimes within the UK, the flexibility of fire as a management tool, and the extent to which one can manipulate its ecological effects. The objective of our paper was to elucidate the effects of fires on heathland and peatland ecosystems without taking a position regarding the wider issues associated with moorland management – our focus was solely on understanding how fire affects these ecosystems. It is essential to address this issue as it is critical in evaluation of current ecosystem management practices and the identification of future options.

Before one proposes a shift in management regime, one ideally needs to understand the range of ecosystem effects the current disturbance regime generates, and the trade-offs any changes could produce. Where such knowledge is lacking, an Adaptive Management approach (Holling 1978) should be adopted. Adaptive Management emphasizes the need for a conceptual model of inter-related ecological structures and processes; identification of areas of uncertainty; ecologically-justified, testable hypotheses about what the outcomes of management change will be given existing uncertainties; a range of potential intervention/change options that can be applied experimentally; and

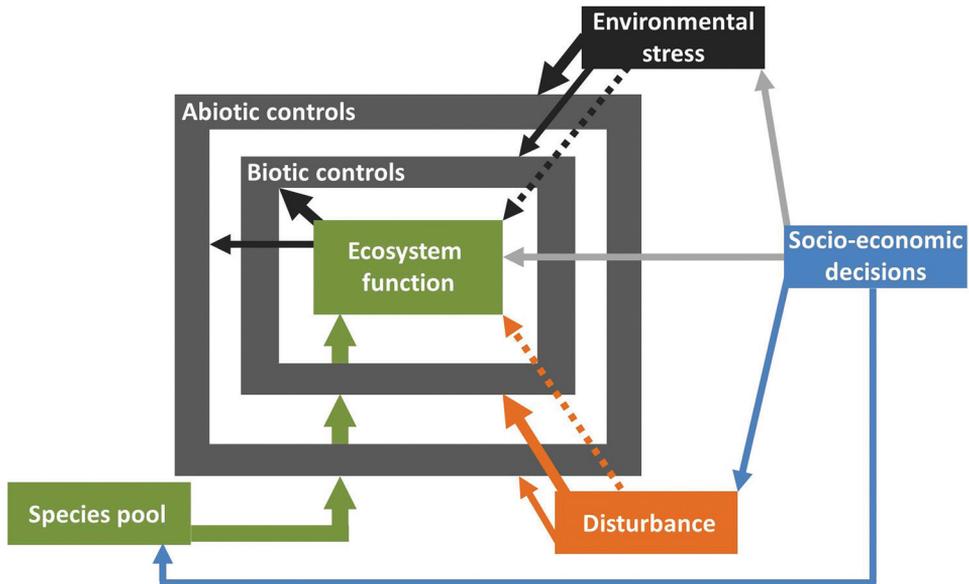


Figure 1. Ecosystem function (including species composition and ecological processes) is controlled by a series of abiotic (e.g. soil type, temperature) and biotic (e.g. species diversity and species’ traits) variables. The abiotic and biotic controls also act as filters controlling the species found at a particular site out of those available from the regional (or historical) species pool. Disturbances, such as managed burning or wildfire, influence both biotic and abiotic variables and therefore ecosystem function. The nature of that influence will depend upon the characteristics of the disturbance regime and the particular ecosystem function of concern. Socio-economic decisions influence the system by impacting directly on disturbance regimes (e.g. via regulation of prescribed burning), the species pool (e.g. by re-introducing locally or regionally extinct species), and environmental stress (e.g. via anthropogenic climate change). Disturbance (fire) effects (orange) were the focus of Davies et al. (2016) whereas socio-economic decision-making (blue) were the focus of Monbiot (2016a). We argue that views in the blue region should not influence the interpretation of scientific data in the orange region. This does not mean socio-economics are not important, but these issues should be addressed in a participatory manner rather than via polemics, which assume one has a monopoly on the “right” answer about ethical, conservation and economic priorities. This diagram was adapted from Halle (2007).

mechanisms that allow the measurement of management effects and the identification of trade-offs such that the conceptual model can be updated and management options expanded or adapted if desired outcomes are not reached (Westgate et al. 2013). Adaptive Management therefore emphasizes “learning by doing” and presents an alternative to wholesale changes followed by reactive responses to problems if/when they occur. Management should not proceed by trial and error or with an unwillingness to acknowledge and account for ecological, social and economic uncertainties.

Monbiot’s criticism could be taken as suggesting that scientists and managers know all they need to about the ecological effects of variation in fire regimes or the ecosystem dynamics of heathlands and peatlands, but this is very clearly not the case

(e.g. O'Brien et al. 2007, Glaves et al. 2013). Monbiot (2016a) says “Is fire good for ‘landscapes that owe their existence to the use of fire as a management tool’? Er, let me get back to you on that”, thus suggesting that we pre-empt the answer to our own question and that we argue that fire is “good”. But there is, in fact, no clear answer to the question he has posed. Monbiot himself appears to be aware that the relationship between moorland ecosystems and fire can be complex and that, contrary to the sentiment expressed in the quote above, certain *fire regimes* can be damaging to these systems. In a previous contribution, Monbiot (2016b) highlighted degradation of moorlands as a result of interactions between fire and grazing. Degradation of peatlands or heathlands by fire is indeed possible but, as we argued in our paper, such processes are often not the sole result of one particular disturbance but rather a result of disturbances outwith the historical norm, e.g. severe wildfires (Maltby et al. 1990, Davies et al. 2012), compounded or interacting disturbances (e.g. Vandvik et al. 2005, Britton and Fisher 2006), or disputed classifications of ecosystem health (see Box 1 in Davies et al. 2016). In Monbiot’s example of the decline in bog and heathland habitats on Dartmoor (Monbiot 2016b), we would suspect that inappropriate combinations of burning and grazing are more likely to be to blame than the use of burning as part of the management of the system *per se*. Previous research has shown the role that heavy grazing has played in the decline of heather-dominated moorlands (e.g. Stevenson and Thompson 1992), whilst areas which retained grouse moor management (and thus managed burning) have shown comparatively small declines compared to other land-uses (Robertson et al. 2001).

Prescribed burning has long been known to influence the behaviour of wild and domestic grazing animals (e.g. Grant and Hunter 1968, Oom et al. 2002) with grazers typically congregating on more recently burnt patches. Where the relationship between area burnt and stocking rates is out of balance this can lead to heavy grazing pressure in the years following burning and the loss of heather cover. Overstocking in general, poorly timed grazing, and burning vegetation that is either too young for the heather to have recovered after the last fire or too old for the heather to resprout can also precipitate heather loss (Anderson and Yalden 1981, Hobbs and Gimingham 1987). Significant variation can exist within and between regional fire regimes, as well as between different types of fire, such as managed burns versus wildfires (Davies et al. 2016), and even within individual prescribed fires (Davies et al. 2010). It would thus be a simplification to argue that fire, or any other disturbance, is “good” or “bad” – one has to consider it in relation to the character of the wider disturbance regime and the ecological functions or features of concern.

2. The ecological value of moorland landscapes

Monbiot clearly has strong views about what ecosystems are appropriate for the British uplands and he has been at the forefront of the nascent “rewilding” movement in the UK (Monbiot 2014a). Some of his ideas have gained a sympathetic hearing amongst

the authors here. Monbiot, however, suggests that we failed to engage with this wider debate about whether anthropogenic ecosystems, such as peatlands and heathlands, are “right” for our uplands. In his comment on our paper, and in previous writings (e.g. Monbiot 2013a, Monbiot 2013b, Monbiot 2014b, Monbiot 2015), he has questioned the ecological value of anthropogenically-derived ecosystems in general, and heathlands and peatlands specifically, in rather strong terms. Many of his contributions mix political and ecological issues in a manner we suggested in our paper was unhelpful when trying to discern the ecological effects of fire. He suggests that we started from an assumption that current conservation priorities, including statutory designation of large areas of heathland, are correct. There are undoubtedly strong arguments to be made for increasing forest and woodland cover in the British Uplands (e.g. Thomas et al. 2015), but it would be incorrect to suggest that heathlands and peatlands hold no or little ecological value, or that one has to choose between these ecosystems and forests at a national or landscape scale. Heathland and bog ecosystems have statutory conservation recognition not just in the UK but in many other regions of Europe (European Commission 2013). The report by Van der Waal et al. (2011) highlights the diverse array of provisioning, regulating and cultural ecosystem services provided by upland and heathland ecosystems in the UK. Douglas et al. (2015) pointed to the overlap between designated areas in the UK uplands and areas with a history of managed burning activity, which, in our view, highlights the role historic management has played in creating some features of conservation importance. Whether current management regimes are appropriate for maintaining the range of ecosystem services that are now desired from upland landscapes is an open question. In our paper we pointed to the fact that several other countries in Europe are actively seeking to reintroduce burning and/or grazing to protect and restore similar habitats in the absence of grouse moor management or any economic incentive from agricultural use (e.g. Keienburg and Prüter 2004, Vandvik et al. 2005, Ascoli et al. 2009). Many ecologists recognize the importance of management for early-successional habitats such as shrublands even in otherwise forested landscapes and in the face of public skepticism about their value (e.g. Askins 2001). Nevertheless, there is considerable debate about the use of fire as a management tool on moorlands and peat bogs even amongst those who believe these habitats are worthy of conservation protection.

3. Species, habitat and ecosystem diversity – the importance of scale

We would agree with previous authors (e.g. Levin 1992, Legg 1995) that management needs to consider the importance of scale in ecology and conservation, and to think about ecological processes and diversity across multiple taxonomic, spatial and temporal scales. This is particularly true when considering the effects of disturbances such as fire or grazing. Ecological responses to management vary across spatial and temporal scales including both between and within landscapes. For example, looking at the short-term effects of grazing removal on upland grasslands has shown initial declines

in species richness in some locations, but the effects were different at higher elevations where species diversity increased when stock was removed (Davies and Bodart 2015). Scale is critical here - if Davies and Bodart had been able to consider longer timescales of decades or centuries, rather than years, and a wider range of bioclimatic settings, their conclusions might have been different (Bakker et al. 2009). Unfortunately long-term and large-scale studies are in woefully short supply.

Contrary to what Monbiot (2016a) appears to suggest, it is simplistic to assume that one can choose the “right” ecosystem simply by counting the number of species a particular habitat contains (Fleishman et al. 2006). Monbiot’s point that birch and pinewoods in the Cairngorms contain a wonderful diversity of species is certainly true (Shaw and Thompson 2006), though few of these are particularly rare internationally (exceptions would include endemics such as the Scottish crossbill, *Loxia scotica*). However, patch-scale (alpha) species diversity is not the only metric by which ecologists evaluate ecosystems. Diversity occurs at a variety of scales of organization and includes, in addition to the local species richness, the diversity of communities and habitats at landscape scales (e.g. Peterson et al. 1998), the diversity of ecosystems globally, as well as genetic diversity within species (e.g. Rao and Hodgkin 2002, Secretariat of the Convention on Biological Diversity 2005). Species diversity responses to management can often be rather specific. For example the response of species richness to birch colonization of moorland (as might occur during “rewilding”) depends upon which species group one considers – plant species richness has been shown to decline but the diversity of *Collembola* and mites increased in the same study (Mitchell et al. 2007). The heterogeneity in habitat structure associated with burning can have important effects. For example in the study by Bargmann et al. (2016), variation in the composition of invertebrate communities meant traditional burning practices increased diversity of this group at the landscape scale. Davies and Legg (2008) found similar effects for lichen species and Velle et al. (2014) for vascular plants.

Diversity in species composition and ecosystem function is just as important as species diversity when making ecological management decisions. Temperate peatlands, including heathlands, moorlands and blanket bogs, are extremely rare in European and global terms and there have been dramatic losses in recent decades (e.g. Blackstock et al. 1995, Robertson et al. 2001). These ecosystems support important functions including carbon storage and sequestration, particularly in blanket bogs (Ostle et al. 2009), and the provision of habitat for internationally important populations of breeding birds (e.g. Stillman and Brown 1994, Thompson et al. 1995). Many of these species, such as golden plover (*Pluvialis apricaria*), lapwing (*Vanellus vanellus*), oystercatcher (*Haematopus ostralegus*), wheatear (*Oenanthe oenanthe*), red grouse (*Lagopus lagopus scotica*), golden eagle (*Aquila chrysaetos*), merlin (*Falco columbarius*) and hen harrier (*Circus cyaneus*) would likely be displaced by conversion to woodland or forest. With regard to ecosystem function, relationships with land management and vegetation structure can also be complex. For instance, shrub and tree encroachment of bogs can presage fundamental changes in their carbon balance (Walker et al. 2016) and changes to land-surface albedo means the climate change implications of forest regeneration can be complex (de Wit et al. 2014).

Making decisions about land-management in anthropogenic landscapes

We of course do not suggest the above points make grouse moors, moorlands in general, or blanket bogs the “right” ecosystem for all of the uplands. However, we know of few ecologists involved in upland management who would not agree that such ecosystems have ecological value, harbor unique species assemblages and should form part of a structurally diverse, holistically-managed landscape. Managers and policy-makers need to be aware of the inevitable trade-offs involved in management change. None of this prevents, or argues against the desirability of, alterations to “traditional” fire use strategies, woodland restoration or even “rewilding” in some parts of the uplands. In some situations win-wins may exist in addition to trade-offs. For example, in a recently published study, Gao et al. (2016) showed that restoring riparian woodland cover in peatland catchments could have important benefits for flood management. Protecting riparian corridors from fire might also mitigate some of the potential impacts of burning on aquatic ecosystems described by Rachmunder et al. (2013). The suggestion that a choice must be made between “rewilding”, restoration, moorland (traditionally-managed or not), or peatlands is therefore artificial as there is significant room for a diversity of upland ecosystems some of which are presently more abundant than others. The idea that a choice must be made between natural and managed landscapes is also illogical. Disagreements about the status and value of anthropogenically-derived landscapes, such as heathlands and peatlands, may stem from differences in philosophical position regarding humans’ place in the “natural world” and a desire to see naturalness as a simple binary concept rather than as a complex gradient (e.g. Machado 2004, Anderson 2005). Whatever management decisions are made in the British uplands, the resulting ecosystems will never be truly “natural”, if the term is intended as “not affected by anthropogenic activities”. Even in the absence of active management, our landscapes and their species pools have developed under millennia of human impacts on both biotic and abiotic conditions. Our landscapes’ Anthropocene future includes biota, biogeochemical cycles, and climates heavily affected by human activities. Challenges for ecosystem management therefore include: i) understanding how species assemblages and ecosystem services are distributed along gradients of naturalness in order to protect and value the full range of ecological diversity; ii) ensuring that the diversity of human socio-cultural perceptions and priorities are reflected in management decision making; and iii) taking an Adaptive Management approach and monitoring ecosystem dynamics so that development along suitable trajectories can be ensured. The assumption that one can reintroduce species, particularly those that have been missing over evolutionary timescales, and necessarily see a “natural” ecosystem state unfold is simplistic, something Monbiot himself seems aware of (Sahn 2014). Again, this does not argue against the potential desirability of woodland restoration or “rewilding”, but management decision-making should be based on ecological knowledge gained through a rigorous application of Adaptive Management.

Finding the right balance between different habitats, such as woodland and moorland, whilst maintaining or enhancing habitat connectivity and minimizing fragmentation will

require landscape-scale approaches to management. We agree with Wynne-Jones (2016), that this in turn requires trust and collaboration between diverse land-owning groups, interest groups, and individuals in making use of the best available evidence of the ecological trade-offs involved. Getting buy-in for management change requires shared knowledge and understanding of the evidence. The right balance between different ecosystems is not for us or any one person or interest to decide. It is an ecological, economic, philosophical and aesthetic decision that needs to be made by society as a whole, respecting the differing stakes and legal rights that people have in these landscapes.

Monbiot (2014a) takes one particular view about what the priorities for future landscape management should be. In his comment on our paper he questions the legitimacy of heathland and peatlands landscapes seeing them as a “reflection of cultural hegemony”, which favours particular interests such as grouse moor owners (Monbiot 2016a). His ecological priorities thus appear to be at least partly politically-motivated – in our paper we specifically requested people to try to set politics aside when discussing ecosystem dynamics. That does not mean that politics and socio-economics cannot play a role in determining land-management priorities, indeed they are vital components of the socio-ecological system that needs to be understood and managed in order to gain desired outcomes (Figure 1). We do however suggest that when specifically discussing ecological dynamics one should try to exercise a degree of self-awareness regarding one’s inherent biases, and try and minimize the extent to which they influence interpretation of environmental data. Contrary to Monbiot’s views we would argue that the fact that peatlands are cultural landscapes (*sensu* Birks et al. 2004) does not mean they are a reflection of the current culture and its associated forms of land-ownership and management. This is merely the latest (and in ecological terms fairly recent) phase in their history and evolution. The classic text by the eminent Charles Gimingham (Gimingham 1972) and the excellent volume by Ian Simmons (Simmons 2003) highlight the long (pre)history of heaths, moors and bogs in the UK. These systems are a reflection of millennia of post-glacial human modifications and climatic changes, extend along the Atlantic regions of Europe from Portugal to northern Norway, and are not simply the outcome of 19th century style grouse shooting in the UK. These are ecosystems in which species have had long enough to evolve to disturbance by fire (Vandvik et al. 2014), and they are a function of the sum total of human management and culture over the last several thousand years.

Where there is a desire to move away from existing land-uses such as grouse moor management and driven grouse shooting, trade-offs between the benefits and dis-benefits of the ‘old’ and ‘new’ forms of management need to be considered. This will need to include acknowledgement that, whatever one’s view about hunting or the wider aspects of moorland management, the significant private financial investment required for any form of ecosystem management or restoration will need to be accounted for (Robertson et al. 2001, Tharme et al. 2001, Sotherton et al. 2009). We suggest that collaborative, inclusive and balanced approaches to landscape scale planning and eco-

system management will minimize conflicts and more successfully leverage the human and financial resources of heathland and peatland stakeholders. Ecological management tools, such as fire, can be used to achieve a diversity of objectives. However, as previous publications have argued (e.g. Davies et al. 2006, Penman et al. 2009), fire use should be ecologically based, bounded by clear objectives and utilized under an Adaptive Framework.

The need for informed, critical, and respectful debate remains

As we stated in our paper, we believe that the current tone of the debate about the use of fire as a management tool is overly simplistic. This is highlighted by the controversy that surrounded the pre-publication release of our paper, with several newspapers and organisations using it as an opportunity to selectively quote us in an attempt to further their own agendas – something we had specifically critiqued in our paper. The involvement of a Public Relations agency, for which YFTB appears to be a “front organization” (*sensu* Smith and Malone 2006, Beder 2014), was particularly troubling as YFTB appears to have been developed for the specific purpose of criticizing the RSPB. We do not believe using PR agencies is an appropriate approach for unbiased dissemination of scientific research nor should research be used as an opportunity to further agendas or propagate conflict.

These behaviours are symptomatic of a lack of respect between different stakeholders at the more extreme ends of the upland management debate and we would urge that further discussion takes place without resorting to language or accusations that could cause offence. Monbiot (2016a) suggested that in our paper we did not engage properly with the article of his we cited because we focused our critique on his title “Meet the conservationists who believe that burning is good for wildlife” and strapline “Our national park authorities are vandals and fabulists, inflicting mass destruction on wildlife and habitats, then calling it conservation”. The relevant section of our paper was specifically focused on the need for constructive debate (it was not about the conservation implications of current or potential future management). We do not think it is unreasonable to suggest that Monbiot’s headline and strapline may have caused offence to dedicated conservationists and land-managers and may not have been particularly effective in promoting a balanced, evidence-based debate. Likewise we were disappointed that the title of Monbiot’s comment on our work, “Bonfire of the verities” (Monbiot 2016a), could be taken to suggest that we were somehow being dishonest in our paper. We are not alone in making such criticisms of some of his writing (Wynne-Jones 2016), though Monbiot has previously emphasized the need for inclusivity and presented his ideas with greater nuance (Stahn 2014). The need to be respectful does not mean it is not legitimate to critique and debate relevant contributions to the scientific or popular press, we just need to do so with a greater degree of respect for differing perspectives.

Conclusion – ecological, participatory, adaptive fire management

We actually think that we and Monbiot are arguing at cross purposes (Figure 1) – whilst his original article was a somewhat politically-motivated higher-level critique of heathland as a valid target for conservation, and therefore of fire as an effective means to manage the landscape, we were concerned with understanding the complex ecosystem effects of fire. In a heated debate like the one surrounding the use of fire as a management tool, it is essential for science communication to be based on facts and data, not emotions and politics. Ironically, both those opposed to burning (seemingly in general, not just in current forms), and those defending intensive grouse moor management practice (such as that can be generalized), have sought to portray our work as defending the *status quo* – something that was never our intention. Instead, we continue to argue for an ecological approach to the use of fire that is based on Adaptive Management principles, scientific evidence, and a clear understanding or hypothesis about how fire can be used to achieve specific aims. In our view, not only is the current debate unconstructive, it is also illogical – debating whether fire has either “benefits” or “impacts” is pointless as it has both, depending on the spatial and temporal scales and ecological values and ecosystem services one considers. As Reed et al. (2013) have already pointed out, we need to move towards an evidence-based assessment of the trade-offs inherent in different management regimes and mechanisms to promote participatory, landscape-scale prioritization of land use.

Unfortunately, the effect of fire on moorland and blanket bog ecosystems is likely to remain a topic of debate well into the future as its knowledge base is still far from adequate and managers are not in the position to make informed trade-offs. For instance, there is poor understanding of the complex interactions between different disturbances (such as fire, grazing, drainage, and nutrient deposition) on carbon cycling, vegetation dynamics, and wildlife habitat utilization, but management decisions have to be made nonetheless. In doing so it is vital that none of us are parochial about the evidence we use and that we do not cherry pick studies which support our own positions.

Many valuable ecosystems owe their structure, function and conservation value to human manipulation of fire regimes (Bowman et al. 2011). Nevertheless, globally, the use of fire as a management tool is not without debate and seeing ecosystems burning arouses strong emotions (e.g. Ryan et al. 2013). Understanding what makes people so passionate about the use (or not) of fire is important (McCaffrey 2006) as there is recognition that, just like conservation grazing (e.g. Plassmann et al. 2010), fire is a valuable part of the ecosystem manager's toolkit (see, for example, Russell-Smith and Thornton 2013 and references therein). Where there is conflict over management it is vital that an Adaptive Management approach is followed (Holling 1978). This emphasizes the importance of monitoring the effects of management and adapting to achieve desired outcomes rather than just ploughing on with traditional approaches, or making wholesale changes, without evidence for the benefits. Crucially, Adaptive Management also stresses the importance of constructive engagement with all stakeholders

and that all stakeholders buy into the principle of evidence-based management. The successful “Bogathon” events organized by the Moorland Association and the Heather Trust in cooperation with Natural England and others are an important example of the positive outcomes of collaboration and cross-sector cooperation (Moorland Association 2015; Natural England 2015). Everybody is entitled to hold strong views and preferences for certain ecosystems on the basis of aesthetics, emotional response, or political outlooks. At the same time, biodiversity and ecosystems are also regulated by national and international regulations and conventions, that mean managers are not completely free to choose which habitats to conserve, restore, or even create in UK landscapes. Once a decision about the conservation or restoration target for a particular area is made, there is a critical need to understand the ecological processes operating in the systems in order to make sound management decisions. We would suggest that it is possible for people from the diverse array of upland interest groups, and those with differing opinions and priorities, to engage in the important debates about the future of ecosystems without insulting each other. After all, a key positive conclusion that can be drawn from these exchanges is that we all care passionately about the future of these landscapes.

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