Rapid reassembly of an intertidal community following prehistoric disturbance

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Abstract

The elimination of lower trophic levels following severe habitat disturbance can trigger new community assembly processes. However, little is known about how past habitat disturbances have affected codependent evolution of trophically-linked and closely interacting taxa. Using genome-wide analysis of a macroalgal community affected by ancient catastrophic coastal uplift, we track the ecological dynamics of past co-dispersal and co-diversification among obligate interacting taxa. Our study reveals rapid and concerted reassembly of an intertidal community following disturbance. Specifically, hierarchical co-demographic analyses of multispecies genomic data support synchronous expansions of four strictly intertidal species in the wake of tectonic disturbance. These data show that tight algal-epifaunal links underpin parallel demographic responses across distinct trophic levels. These results highlight that high-resolution comparative genomic data can elucidate the strength of obligate ecological interactions, and the evolutionary dynamics of past co-dispersal and co-diversification in post-disturbance communities.

Introduction

The structure and dynamics of ecological communities can be profoundly influenced by environmental disturbance (Sousa 1984; Pickett *et al.* 1989; Newman 2019). Specifically, when disruption eliminates populations from a habitat patch, a new community assembly process will be initiated (Fukami 2015). While most studies of community assembly are limited to real-time observations of contemporary events (e.g. Minshall et al. 1983; Aquilino and Stachowicz 2012; Konar 2013; Hérault and Piponiot 2018; Seabloom et al. 2020), genetic and genomic analyses have the potential to provide key insights into community-level processes and responses to disturbances over broader temporal and spatial scales (Hu et al. 2009; Salces-Castellano et al. 2020). Previous multispecies genomic analyses, for instance, have highlighted the potential of such broad approaches to elucidate large-scale (e.g. community-level) demographic and/or evolutionary biogeographic shifts (e.g. Bunnefeld*et al.* 2018; Cole *et al.* 2019). Such analyses can potentially bridge the gap between community dynamics and microevolutionary processes, enhancing our understanding of community responses to rapid environmental change (Johnson and Stinchcombe 2007; Stone et al. 2012; Cavender-Bares et al. 2016).

Obligate interacting (e.g. trophically linked) taxa that coexist within a community are expected to show concordant responses to habitat disturbance. The host-tracking hypothesis, for instance, predicts that if pairs of closely interacting species such as epibionts or parasites pursue the range shift of their host, parallel genetic signatures of spatial expansion should be observable across the interacting species (Schluter 2000; Kohnen *et al.* 2012). Such patterns of geographic co-diversification can arise either synchronously (Becerra 2003; Wheat et al. 2007) or with a temporal delay (Hayward and Stone 2006; Stone et al. 2009; Stone et al. 2012). When disturbance events disrupt ecosystem structure, the extent of temporal delay between expansions of host and dependent taxa can strongly influence the formation of mosaic assemblages across space and time (Thompson 2005; Hoberg & Brooks 2008; Hoberg *et al.* 2012).

Large habitat-forming macroalgae support diverse benthic communities and act as the foundations of facilitative and/or trophic interactions (Schiel & Foster 2015). A variety of environmental stressors can affect the population dynamics of habitat-forming macroalgae and subsequently alter the community dynamics of kelp forests. Such complex interactions have been traced in the effects of contemporary habitat disruptions such as heat waves on both forest-forming macroalgae (Wernberg *et al.*2018; Gurgel *et al.* 2020; Smale 2020) and their associated macroinvertebrate communities (Ettinger-Epstein & Kingsford 2008; Smale*et al.* 2017). Previously, genetic data have revealed that historical habitat perturbations can underpin phylogeographic structuring of intertidal macroalgae (Parvizi *et al.* 2019, 2020), although the effect of such disturbances on the dynamics and assembly of kelp-associated benthic communities (epibiota) remains unclear. In the present study, we carry out new genomic analyses at the macroinvertebrate community level to test for multi-species responses to a major historic disturbance caused by coastal uplift approximately 900 yr BP. We test the following hypotheses: (i) habitat disturbance drives concordant spatial genetic shifts in kelp and epibiota (co-diversification), (ii) hosts and epibiota underwent concerted recolonization of disturbed patches.

Materials and methods

Study area

The Akatore Fault is the most seismically active area on the southeast coast of New Zealand's South Island (Figure 1). The onshore portion of this fault has, in the past millennium, uplifted an approximately 30 km of the coast by 2-3 meters above the high-tide zone (Litchfield and Norris 2000). This amount of coastal uplift is reported to be sufficient to eliminate intertidal species and potentially create empty habitats for recolonization (Jaramillo *et al.* 2012; Hamling *et al.*2017). Radiocarbon dating at the Akatore fault line has constrained the most recent rupture event to 800-1000 yr BP (Litchfield & Norris 2000; Craw *et al.* 2020). Additional radiocarbon dating from sea caves at the palaeo-hightide level similarly provided age estimates <1000 years old, confirming direct relationships between earthquake and coastal uplift (Craw *et al.* 2020; Parvizi *et al.* 2020).

Study taxa

Previous analyses have revealed striking genomic signatures of post-uplift colonization in populations of intertidal habitat-forming macroalgae *Durvillaea poha* and *D. antarctica* in southern New Zealand (Parvizi *et al.* 2020), but the impacts of uplift on associated epifaunal populations remains unknown. In the present study, we analyze three epifaunal macroinvertebrates inhabiting intertidal*Durvillaea* 's holdfasts. We focus on non-dispersive, brooding epifaunal taxa exhibiting continuous (versus patchy) distributions along both uplifted and non-uplifted sites. Previous studies of intertidal*Durvillaea* holdfast communities indicate that the chiton*Onithochiton neglectus* , the amphipod *Parawaldeckia karaka* , and the isopod *Limnoria segnis* have tight ecological links to their host macroalgae and are potentially highly vulnerable to coastal disturbance (Nikula *et al.* 2010; Fraser *et al.* 2011; Waters *et al.* 2018; Salloum *et al.* 2020). Specifically, these benthic macroinvertebrates are brooders, obligate holdfast dwellers, and are restricted to macroalgae for reproduction, grazing and dispersal.

Sampling and genomic data acquisition

Holdfast epibiota were collected from intertidal *Durvillaea*distributed along the uplifted rocky shores of the Akatore region as well as its northern and southern flanking non-uplifted coasts (Fig. 1). This spatial sampling of invertebrates was closely aligned to previous sampling regimes for their *Durvillaea* host species to facilitate precise genomic comparisons of both macroalgae and epifauna. Accordingly, we carried out a fine-scale sampling (sampling every 2-6 km to exclude non-habitable sandy beaches) from within an approximately 100 km of coastline (Figure 1; Table S1). As our studied invertebrates can move between *D. poha* and *D. antarctica* (but not *D. willana* , which has a more dense holdfast free of burrowing invertebrates) we randomly collected samples from both hosts at different sites. To reduce the effect of including closely related individuals in our genetic analyses we analyzed samples from multiple holdfasts at each site (Nikula *et al.* 2010). Details of laboratory procedures and single nucleotide polymorphism (SNP) acquisition are described in the Supplementary Methods and Table S2. The final high quality SNP dataset consisted of

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13991 SNPs for *O. neglectus* , 4809 SNPs for *L. segnis* and 8162 SNPs for *P. karaka* . In addition to the holdfast invertebrate datasets, we retrieved the previously generated VCF files for all three *Durvillaea*species from Parvizi et al. 2020 (available at https://datadryad.org/stash/dataset/doi:10.5061/dryad.pg4f4qrkm) and reanalyzed them to have a consistent analytical approach when comparing the population genomic structure and demographic history of hosts and epifauna.

Spatial genomic structure along uplift vs. non-uplift habitats

We performed several approaches to document the extent of genetic differentiation among uplifted versus non-uplifted sites and to characterize uplift associated genetic structuring in the holdfast epifauna. We used principal component analysis (PCA) to explore SNP variation among individuals for each species separately using the R package *adegenet* v.2.1.1 (Jombart 2008). We applied the spare non-negative matrix factorization (sNMF) algorithm implemented in the R package LEA v.2.8.0 (Frichot *et al.* 2014; Frichot & Francois 2015) to infer individual ancestry coefficients and delineate putative genomic clusters. We tested for 1-15 ancestral populations (K) with 50 replicates per each K value and chose the best K by using a cross-entropy criterion. To evaluate the robustness of our results we ran the analysis using four values for the alpha regularization parameter (1, 10, 100 and 1000). Bar plots were visualized using the R package *pophelper* v.2.3.0 (Francis 2017). We inferred phylogenetic relationships among populations by constructing neighbor joining trees using SplitsTree v.4.16.1 (Huson & Bryant 2006).

Uplift associated demographic history

We used multidimensional folded site frequency spectrum (mSFS) to infer post-uplift recolonization dynamics using the continuous-time coalescent simulator fastsimcoal v.2.6 (Excoffier *et al.* 2013) on those species that showed a distinct cluster in the uplifted region. Based on the clustering results we defined three-population models for *D. poha* and *L. segnis* (i.e. North, Uplift, and South lineages) and four-population models for *D. antarctica* and *O. neglectus*(i.e. Far North, Nearby North, Uplift, and South lineages; see Supplementary Methods and Fig. S7-S8 for details).

Given the absence of pre-quake genetic data for the studied species, we considered a constant population size for all non-uplift lineages and characterized all models by a bottleneck event at the time of the earthquake. For each demographic model we performed 50-100 independent runs of 500,000 genealogical simulations and 40 cycles of Brent algorithm to estimate the expected SFS and composite likelihood for a given set of demographic parameters. We chose the best fit recolonization scenario by calculating the Akaike Information Criterion (AIC) and Akaike's weights.

To infer the degree of synchrony in size change among the uplift lineages of the host kelps and their epifauna we performed a hierarchical co-demographic modeling using the R package*Multi-DICE* (Xue & Hickerson 2017). We first projected down the SFS of each 'uplift' lineage to 38 haploid individuals. We simulated 100,000 scenarios with species expanding from a relative low population size by a factor 100 - 10,000. Effective population size before expansion was constrained between 100 and 1000. Species were considered co-expanding in scenarios where their expansions started within the same 50 years (τ buffer prior = 50 years). Additionally, a more relaxed 200 years co-expansion threshold (τ buffer prior = 200 years) was applied in a different set of simulations. In order to infer the most likely scenario, the proportion of co-expanding species, ζ, and the timing of the expansion events, τ, we generated the aggregate site frequency spectrum (aSFS; Xue and Hickerson 2015) for each simulation. We used R to sample the best 5% of the simulations of the aSFS (5000 simulations) using the rejection method implemented in the *ABC* package (Csilléry *et al.* 2012). We visualised the fit of the observed aSFS within the retained simulations using a PCA produced with the R package *ade4* (Dray & Dufour 2007).

Results

Uplift-associated population structure

PCAs and neighbor joining trees revealed populations in the uplift zone form genetically distinct clusters in both *L. segnis* and *O. neglectus* . These findings were further confirmed by sNMF results where the K

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with the lowest cross entropy value ($K = 4$) revealed spatial structuring closely associated with the Akatore uplift zone for both species. In the amphipod *P. karaka* , by contrast, virtually no population structure was detectable along the relevant coastlines (Fig. 2; Fig. S1-S3). Overall, the strong uplift-associated genetic structure in strictly intertidal epifaunal species (*L. segnis* and *O. neglectus*) closely matches that of their intertidal macroalgal hosts (*D. antarctica* and *D. poha* ; Fig. 2; Fig. S1-S6). In all four of these strictly intertidal species, a shallow yet distinct genetic cluster is tightly linked to the Akatore Fault boundaries (from Taieri Island in the north to Toko Mouth in the south; Fig. 1). Additionally, in both intertidal hosts and their epifauna, genetic admixture is detectable only at the fringes of the uplifted region (Fig. 2).

Recolonization routes of intertidal species

Coalescent simulations showed that epifaunal species recolonized disturbed intertidal habitats from northern source populations (Table S3-S4). Specifically, for *L. segnis* , the best demographic model was recolonization from the North (AIC weight = 0.72). In *O .neglectus* the most supported model showed the uplift lineage has evolved through an admixture event between the Far and Nearby Northern lineages (AIC weight = 0.51). For the host species, the results from fastsimcoal simulations agreed with the previously published estimates of recolonization using approximate Bayesian computation (Parvizi *et al.* 2020). *Durvillaea poha* is inferred to have recolonized the uplifted coasts via admixture between northern and southern source populations (AIC weight = 1) while in *D. antarctica* an admixture between the two northern source populations has resulted in the evolution of the uplift lineage (AIC weight = 0.77). For all four species, the recolonization events are estimated to have occurred approximately 900 years ago, in line with carbon-dating estimates of Akatore Fault rupture (Table S5).

Hierarchical-codemographic modelling using *Multi-DICE* supported a concerted post-earthquake recolonization (τ mode = 953 y BP; τ mean = 791 y BP; τ median = 825 y BP) with support for all intertidal and epibiotic species co-expanding within a 50 year period (Fig. 3). A more relaxed co-expansion threshold of 200 years also supported synchronous expansion of all four species which was estimated to have occurred 913 y BP (τ mode = 913 y BP; τ mean = 736 y BP; τ median = 747 y BP; Fig. S9-S10).

Discussion

Disturbance driven co-diversification of host and epibiota

Genomic analyses reveal that past habitat disturbance has strongly shaped contemporary patterns of genetic variation among populations of interacting intertidal taxa. In the current study, both intertidal seaweeds (*D. antarctica* and *D. poha*) and their obligate epifauna (*L. segnis* and *O. neglectus*) show abrupt shifts in genotype composition that are both spatially and temporally linked to historic tectonic disturbance. These multispecies signatures thus highlight community-wide effects of large-scale ecological disturbance. Indeed, direct observations from recent coastal uplift events in New Zealand and Chile have reported that vertical displacement of tidal zone causes widespread extinction of intertidal macroalgae, creating substantial new intertidal habitats for recolonization (Castilla 1988; Ortega *et al.* 2014; Clark *et al.* 2017; Schiel *et al.* 2019). Our genomic findings confirm an historic uplift-driven elimination of intertidal macroalgal communities, followed by rapid and parallel recolonization of empty intertidal habitats. These strong and concordant genomic signatures of historic disturbance persist to present because early-recolonizing lineages can reach high densities and subsequently exclude late-arriving individuals (Ibrahim *et al.*1996; Waters *et al.* 2013; De Meester *et al.* 2016), thus facilitating strong genetic differentiation between ancestral versus newly colonized areas (Excoffier *et al.* 2009).

Concerted recolonization and co-dispersal of host and epibiota

Despite the potential challenges of inferring fine scale temporal differences in expansion timing among species (Gehara *et al.*2017), the different τ pulse buffer priors we used in the *MultiDice* analysis in addition to the *post hoc* comparison of independent fastsimcoal simulations consistently supported synchronous, post-uplift demographic expansions across the *Durvillaea* hosts and their specialized consumer species. These finding highlight rapid biological responses to disruption, and indicate that community reassembly can be concerted

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when taxa have tight ecological links. These findings also support the contemporary host-tracking hypothesis, showing that temporal patterns of lineage diversification are strongly congruent across different trophic levels (Becerra 2003; Nicholls *et al.* 2010). Although our studied species are co-distributed and can be subject to similar environmental changes and vicariance events, the inferred synchronous demographic expansion indicates a strong ecological interdependency between the macroalgal hosts and their holdfast epifauna.

Macroalgal rafting is considered an important dispersal mechanism in the assembly of biological communities of isolated coastal ecosystems (Thiel & Gutow 2005; Fraser *et al.* 2011; Gillespie *et al.* 2012; Nikula *et al.* 2013). Buoyant *Durvillaea* macroalgae, in particular, have high rafting propensity (Fraser *et al.* 2011) and, when detached, can retain diverse epifaunal macroinvertebrate assemblages that have the potential to survive and even brood throughout their rafting journey (Miranda & Thiel 2008; Waters *et al.* 2018). In particular, holdfast-burrowing epibiota such as *Limnoria* and *Onithochiton* , which have no planktonic larvae and limited autonomous dispersal capacity, are expected to rely heavily on their rafting hosts for dispersal. In keeping with this prediction, our multi-population demographic modelling reveals a tight co-dispersal pattern whereby uplifted coasts were broadly colonized from northern source populations. While this dispersal route runs counter to prevailing offshore winds and currents, previous studies have shown that strong storms and surface waves can underpin counter-current dispersal in rafting assemblages (Fraser *et al.* 2018b).

The spatial genomic structure of the intertidal *Durvillaea* hosts, *L. segnis* and *O. neglectus* indicates a higher admixture between the uplift and non-uplift clusters in the invertebrates compared to the kelps. Such patterns of local admixture may reflect the more extended opportunities for local, active dispersal in invertebrates among neighboring locations, and/or their patchier local distributions which may provide more opportunities for the establishment of dispersing individuals. In contrast, the densely populated kelps prevent the establishment of dispersing recruits and restrict effective gene flow through high-density blocking (Waters *et al.* 2013).

Species-specific responses to tectonic disturbance

Species responses to environmental perturbations can be strongly governed by life-history strategies and habitat requirements (Sousa 1984; Ewers & Didham 2006). Although disturbances are critical for liberating new territories for recolonization, the survival of small refugial patches can still inhibit population genomic turnover in the disturbed patch (Fraser *et al.* 2018a). In our study, two species that tolerate subtidal conditions showed little or no evidence of historic disturbance. Specifically, only limited structuring was detected in the subtidal kelp *D. willana* . Additionally, the facultatively subtidal amphipod, *P. karaka* , was represented as a single, broadly panmictic population. This amphipod has enhanced swimming potential in water column (Fincham 1974; Lowry & Stoddart 1986) and has been reported from deeper sublittoral zones (Lowry & Stoddart 1983). These characteristics have possibly facilitated the survival of *P. karaka* through the uplift event by promoting host-switching to non-disturbed subtidal macroalgae such as *Macrocystis pyrifera* (Alonso 2012). On the contrary, while the chiton, *O. neglectus,* has the potential to survive under boulders on rocky shores (Salloum *et al.* 2020), the populations in Akatore did not persist through the coastal uplift and disruption of the *Durvillaea* hosts has left a significant genomic signature in the chiton populations. These findings suggest that microhabitat and dispersal ability can substantially influence species' responses to major disturbance.

In summary, multispecies demographic analyses reveal a remarkably synchronous and concerted community-wide response to large-scale prehistoric disturbance. Moreover, our findings indicate that community-level genomic studies present a key approach for tracking the effects of major ecological perturbations increasingly expected under global change scenarios (e.g. Shive et al. 2018; Newman 2019; Ward et al. 2020).

Acknowledgements

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Data accessibility statement. The genomic data and metadata, demographic models' scripts and R codes will be archived in Dryad.

Figure legends

Figure 1. (a, b) Sampling details of macroalgae and epibiota. Colors on the map show the sites that were affected by the Akatore earthquake (red) and non-uplift sites to the north and south of the uplifted rock platforms. Location codes are given in the Table S1. (c) An example of devastating consequences of coastal uplift on macroalgal communities in which the intertidal *Durvillaea* suffered regional extirpation. Photo: C.I.F., Ward Beach, November 2016. (d) The holdfast of intertidal *Durvillaea* harbors diverse benthic communities and their tight ecological links make the epibionts potentially highly vulnerable to coastal uplift too.

Figure 2. The evolution of spatial genomic sectors along the coast uplifted 900 yr BP in intertidal *Durvillaea* hosts and their obligate epifauna. Bar plots show optimal K (number of inferred ancestral populations) from sNMF clustering analysis and the 'uplift' cluster is shown in red. The sites that were affected by the Akatore earthquake are shown between dashed lines and populations are ordered from north to south in all bar plots (see Fig. S1-6 for more details). Neighbor-joining trees represent the 'uplift' populations as separately evolving lineages in the intertidal *Durvillaea* and their obligate and strictly intertidal epibiota.

Figure 3. Hierarchical co-demographic modelling supports synchronous expansions of four strictly intertidal species in the aftermath of coastal uplift disturbance. (a) Distribution of the time parameter, τ, for co-expansion (τ mode = 953 y BP; τ mean = 791 y BP; τ median = 825 y BP). Results are based on the τ buffer prior of 50 years. (b) Distribution of the proportion of co-expanding species supporting the co-expansion of all four analyzed species (ζ = 1).

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