

Connectivity structures local population dynamics: a long-term empirical test in a large metapopulation system

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Abstract. Ecological theory predicts that demographic connectivity structures the dynamics of local populations within metapopulation systems, but empirical support has been constrained by major limitations in data and methodology. We tested this prediction for giant kelp *Macrocystis pyrifera*, a key habitat-forming species in temperate coastal ecosystems worldwide, in southern California, USA. We combined a long-term (22 years), large-scale (~500 km coastline), high-resolution census of abundance with novel patch delineation methods and an innovative connectivity measure incorporating oceanographic transport and source fecundity. Connectivity strongly predicted local dynamics (well-connected patches had lower probabilities of extinction and higher probabilities of colonization, leading to greater likelihoods of occupancy) but this relationship was mediated by patch size. Moreover, the relationship between connectivity and local population dynamics varied over time, possibly due to temporal variation in oceanographic transport processes. Surprisingly, connectivity had a smaller influence on colonization relative to extinction, possibly because local ecological factors differ greatly between extinct and extant patches. Our results provide the first comprehensive evidence that southern California giant kelp populations function as a metapopulation system, challenging the view that populations of this important foundation species are governed exclusively by self-replenishment.

Key words: colonization; demographic connectivity; dispersal; extinction; giant kelp, *Macrocystis pyrifera*; isolation; metapopulation; patch; persistence; population dynamics; remote sensing; time series.

INTRODUCTION

Theoretical models of spatially structured populations indicate that demographic connectivity among habitat patches can strongly influence local (within-patch) population dynamics. Dispersal among patches may reduce the probability of local extinction by increasing population growth (Pulliam 1988), decreasing population fluctuations by buffering against stochasticity (Stacey and Taper 1992), or reducing inbreeding depression (Saccheri et al. 1998). Alternatively, widespread dispersal may enhance the probability of local extinction by increasing the loss of individuals or propagules during or soon after transport (Hanski and Zhang 1993, Burgess et al. 2012), or by synchronizing temporal dynamics across the metapopulation, which enhances the likelihood of simultaneous local extinctions (Heino et al. 1997).

Despite these and other important theoretical advances, understanding how demographic connectivity affects local population dynamics in real metapopula-

tion systems remains a central challenge (Hanski 1999, Sale et al. 2006, Eaton et al. 2014). While there have been several careful empirical evaluations, progress has been restricted by three major limitations in data and methodology. First, in most empirical metapopulation studies, estimates of local population abundances and fecundities are usually constrained or contain significant discontinuities over time and space, and thus fail to census all local populations of interest (López-Duarte et al. 2012, Ojanen et al. 2013, Burgess et al. 2014). Moreover, population estimates are often generated with nontrivial detection error or are assumed to follow simple scaling rules (Hanski 1999, Eaton et al. 2014). Second, delineations of patch boundaries commonly fall victim to the mega-patch problem, the difficulty of characterizing distinct, independently fluctuating subpopulations within a single contiguous patch (Holt 1992, Cavanaugh et al. 2014). Third, connectivity estimates are often based on potentially unrealistic assumptions, such as simple dispersal rules or idealized dispersal kernels (Hanski 1999, Kleinhans and Jonsson 2011). Such simplifications are especially troublesome for passively dispersing organisms subject to physical

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advection, such as air- or waterborne propagules (Ouborg and Eriksson 2004, Watson et al. 2010, 2012).

Metapopulation processes may be particularly important to local populations in coastal marine ecosystems because many species have planktonic propagules (e.g., spores, eggs, larvae) with the potential for large and variable dispersal among patchy habitats (Sale et al. 2006). Nevertheless, demographic connectivity in the sea is poorly understood relative to that on land (Sale et al. 2006), largely due to the difficulties of thoroughly censusing local populations and reliably estimating dispersal (López-Duarte et al. 2012, Burgess et al. 2014). Metapopulation theory is increasingly being considered in the design and assessment of marine protected areas (Guichard et al. 2004, Watson et al. 2011), but linking demographic connectivity to local population dynamics remains a major source of uncertainty in the understanding and management of marine populations (Lipcius et al. 2008, López-Duarte et al. 2012, Burgess et al. 2014).

We focused our efforts on the giant kelp *Macrocystis pyrifera*, a key habitat-forming species in temperate coastal ecosystems worldwide, because it is uniquely suited for testing predictions from metapopulation theory. Many attributes of giant kelp make it an ideal study organism, including high population growth rates, short generation times, rapid responses to environmental conditions, strong habitat specialization, patchy and relatively stable habitat distributions, sessile adults, and frequent extinctions and colonizations (Reed et al. 2006a). Furthermore, several recent methodological advances have provided unprecedented spatiotemporal range, resolution, and accuracy in measures of giant kelp population dynamics, habitat availability, and propagule dispersal (Alberto et al. 2011, Cavanaugh et al. 2011, 2014). Moreover, despite much indirect evidence for metapopulation dynamics, plants and algae are greatly understudied in the context of metapopulation theory (Ouborg and Eriksson 2004, Reed et al. 2006a).

We evaluate the hypothesis that giant kelp populations in southern California, USA, function as a metapopulation system by empirically testing the influence of demographic connectivity on local population dynamics. Our analysis overcomes several shortcomings of previous evaluations of metapopulation theory by incorporating abundances derived from a long-term, large-scale, high-resolution census of local populations; novel patch delineation methods that surmount the mega-patch problem; and an innovative connectivity measure that combines fecundity (i.e., biomass) of source populations with estimates of oceanographic transit times derived from a regional ocean circulation model. We used these developments to quantify the location and size of each patch, and measure changes in connectivity and local population dynamics. We then generated a series of statistical models to test the influence of connectivity on probabilities of patch occupancy, local extinction, and colonization.

METHODS

Study system

Macrocystis pyrifera is a fast-growing marine alga that forms dense, highly productive forests on shallow (5–30 m) subtidal reefs in temperate seas worldwide (Graham et al. 2007, Schiel and Foster 2015). In southern California, shallow rocky reefs (i.e., patches) are patchily distributed along the mainland coast (Fig. 1A, B) and vary greatly in their size (Fig. 1C), imposing pronounced spatial structure on giant kelp populations. Due to environmental and demographic stochasticity, local abundances of giant kelp are highly dynamic (Parnell et al. 2010, Cavanaugh et al. 2011, Schiel and Foster 2015) and local extinctions are frequent (Fig. 2; Reed et al. 2006a).

Following local giant kelp extinction, patches are colonized primarily by microscopic spores that are released throughout the year by mature sporophytes (the large, conspicuous stage; Reed et al. 1996, 1997) and passively dispersed by ocean currents (Reed et al. 2004, Gaylord et al. 2006). Because giant kelp spores have relatively short competency times (typically <24 h; Reed et al. 1992) and rapid settlement (hours to days; Gaylord et al. 2006), the vast majority of spores disperse a distance ranging from meters to a few kilometers (Reed et al. 2004, Gaylord et al. 2006, Alberto et al. 2010). For successful fertilization, male and female spores must settle in very close proximity (i.e., millimeters; Reed 1990, Reed et al. 1991), further reducing the likelihood of successful long-distance recruitment. Consequently, dispersal of giant kelp spores among patches is not limited enough to preclude demographic connectivity, yet not broad enough to result in panmixia (Alberto et al. 2011, Cavanaugh et al. 2013).

We focused on giant kelp populations along approximately 500 km of mainland coastline in southern California, USA (Point Purisima to the USA–Mexico border; Fig. 1A), because of three major advantages afforded by the quality and quantity of data from this region. First, accurate censuses of local populations can be derived from a novel 30-yr time series of remotely sensed giant kelp abundance (Cavanaugh et al. 2011). Second, a unique application of graph theory has provided patch delineations that overcome the mega-patch problem (Cavanaugh et al. 2014). Third, spatially realistic dispersal probabilities can be estimated using a regional ocean circulation model (Mitarai et al. 2009, Simons et al. 2013).

Measurements of giant kelp abundances

We measured giant kelp population abundances using satellite-derived estimates of biomass (data *available online*).⁷ Giant kelp forms a floating surface canopy observable from above, providing an excellent opportunity for remote sensing of population dynamics. Briefly,

⁷ <http://dx.doi.org/10.6073/pasta/329658f19d5e61dda0be5ee883cd1c41>

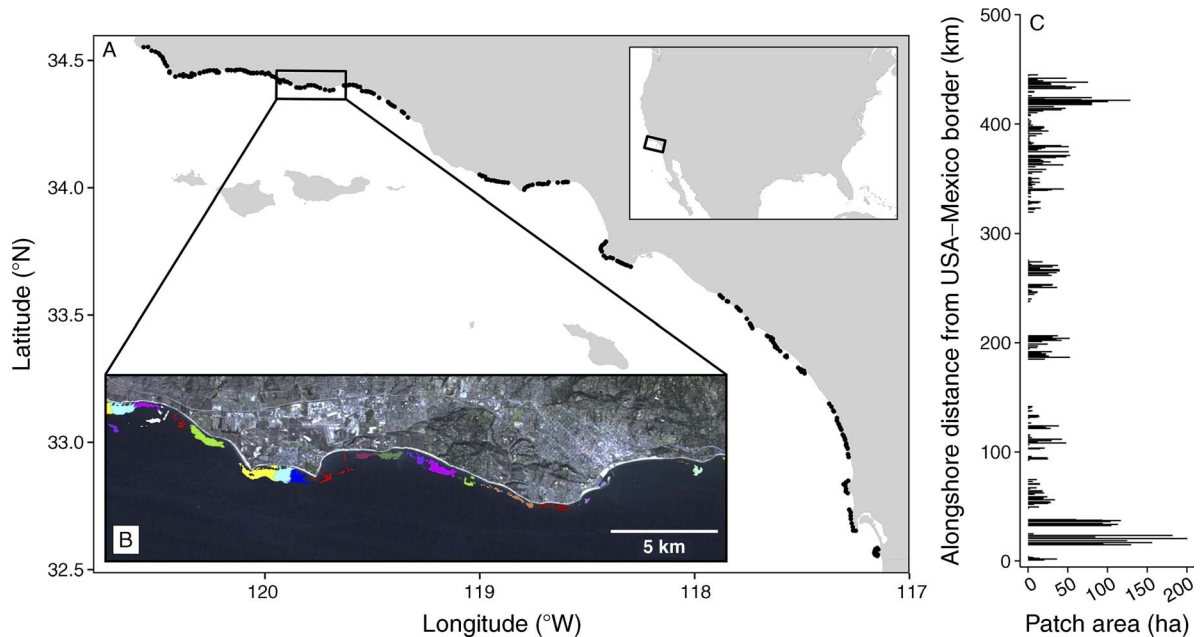


FIG. 1. (A) Map illustrating the distribution of giant kelp (*Macrocytis pyrifera*) patches ($n = 223$) along the mainland coast of southern California, USA (points indicate patch centroids and are not to scale). (B) Inset shows the distribution of giant kelp patches near Santa Barbara, California, based on a graph theory community detection method (each patch is mapped in a different arbitrary color over a Landsat 5 TM satellite image; note the delimitation of patches within mega-patches). (C) The size of each patch, arranged by alongshore distance from the USA–Mexico border. In all panels, the location and size of patches are based on analyses of Landsat 5 TM imagery (1984–2011; see Cavanaugh et al. 2014).

we used 30-m resolution multispectral Landsat 5 Thematic Mapper (TM) and Landsat 7 Enhanced Thematic Mapper Plus (ETM+) satellite imagery to measure kelp canopy biomass density (wet kg/m^2 ; calibrated by diver surveys) across the region at least every 16 d from 1984 to 2014 (Fig. 1B; see Cavanaugh et al. [2011] for a more detailed description of these methods). We used canopy biomass as an estimate of adult population abundance because these two variables are strongly correlated ($P < 0.001$; $R^2 = 0.85$; Cavanaugh et al. 2013).

Patch delineations and the mega-patch problem

Patch boundary definitions are a critical component of any metapopulation model because they determine patch size, connectivity, and rates of extinction and colonization, yet patch delineations are often chosen arbitrarily. Most patch delineations use simple metrics, such as minimum distance or habitat contiguity, which can fall victim to the mega-patch problem: consolidating adjoining but independently fluctuating subpopulations into a single population within a contiguous mega-patch (Holt 1992, Cavanaugh et al. 2014). Aggregating subpopulations within mega-patches causes artificially high variability of within-patch synchrony and artificially low among-patch connectivity and extinction rates. To overcome the mega-patch problem, we used a graph theory community detection approach to classify each Landsat 5 TM pixel into a number of

sub-patches detected within each mega-patch (Fig. 1B). This hierarchical method incorporates suitable habitat area (all areas containing kelp at some point in the Landsat 5 TM imagery; 1984–2011) and population synchrony to generate optimal, spatially explicit patch definitions (see Cavanaugh et al. [2014] for a more detailed description of these methods). Using this technique, we delineated 223 patches in the study region (Fig. 1A).

After delineating patches, we measured patch size as the composite patch area containing kelp over the 30-yr time series. Patches ranged in size from 0.18 to 199.53 ha (Fig. 1C). Because bigger patches tend to support larger populations and experience greater within-patch environmental heterogeneity, theory predicts that populations within them are less likely to go extinct (MacArthur and Wilson 1967, Holt 1992). Bigger patches may also boost colonization rates by offering a larger target area for propagule settlement (MacArthur and Wilson 1967). Moreover, the influence of patch size on local populations is a major consideration in conservation and habitat mitigation, such as the design of marine protected areas (Watson et al. 2011) or artificial reefs (Reed et al. 2006b).

Local population dynamics

Although Landsat imagery is produced at least every 16 d, occasional cloud cover creates unequal numbers of kelp canopy observations across locations and months.

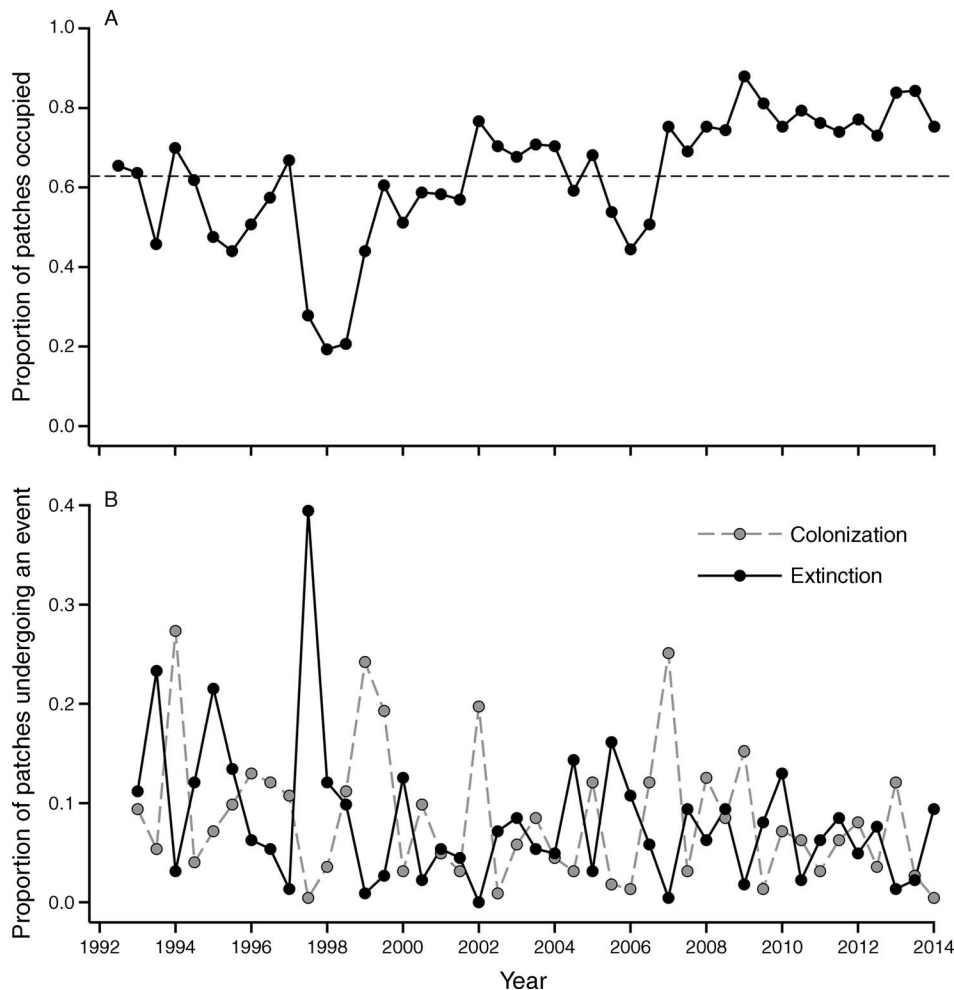


FIG. 2. (A) Time series of the proportion of giant kelp patches ($n = 223$) occupied along the mainland coast of southern California, USA, from the second semester (July–December) of 1992 to the first semester (January–June) of 2014. The horizontal dashed line indicates the average proportion (0.63) over the 22-year period. (B) Time series of the proportion of giant kelp patches that were colonized or went extinct in each semester (six-month period).

To standardize sample size over space and time, we calculated mean canopy biomass within each patch twice per year (January–June and July–December). We restricted our analysis of population dynamics to a 22-yr (44-semester) period from the second semester of 1992 to the first semester of 2014 with completely crossed, balanced observations over space and time (i.e., ≥ 1 measurement of canopy biomass for every patch in every semester; mean number of biomass measurements per patch per semester = 6.9 ± 3.1 [SD]; range = 1–15).

Next, for each patch and semester, we determined giant kelp occupancy (canopy biomass > 0) and then described local population dynamics by enumerating events of extinction (i.e., the transition of a patch from an occupied state (1) to an unoccupied state (0); represented as 1→0), persistence (1→1), colonization (0→1), and colonization failure (0→0) between all pairs of consecutive semesters. We classified a patch as extinct when canopy biomass was undetected for at least one

semester because individuals that survive environmental stochasticity typically regrow surface canopies within six months (Dayton et al. 1984, Schiel and Foster 2015). Conversely, we classified a patch as persistent when it was occupied for two or more successive semesters. Our approach allowed us to census all local extinctions and colonizations, as well as measure durations of extinction and persistence (i.e., numbers of consecutive semesters of giant kelp absence and presence, respectively).

Oceanographic modeling of spore dispersal

To estimate demographic connectivity among patches, we employed Lagrangian (water-following) particle simulations using solutions from a high-resolution (1-km horizontal), three-dimensional ocean circulation model (Regional Oceanic Modeling System, ROMS; see Dong et al. [2009] for model construction and validation). ROMS solutions for the Southern California Bight (Point Purisima to the USA–Mexico border;

Fig. 1A) were available from 1996 to 2007. We released over 500 million Lagrangian particles every 12 h at 5–30 m depth (in 5 m increments) from 135 approximately rectangular nearshore ROMS connectivity cells (nominal alongshore distance = 8 km; mean area = 77.3 ± 5.7 km²). We used the resulting trajectories to estimate the monthly probability of a water parcel arriving at a recipient ROMS cell (j) from each source ROMS cell (i ; $i \neq j$) given an advection timescale (see Mitarai et al. [2009] and Simons et al. [2013] for a more detailed description of these methods). We then determined the minimum mean transit time connecting source and destination ROMS cells as a single metric for water-parcel connectivity (shorter transit times are more connected than longer ones; Mitarai et al. 2009, Watson et al. 2010, Alberto et al. 2011). We repeated this process for each month from 1996 to 2007 and calculated the average water-parcel connectivity among all months.

Because ROMS connectivity cells are much larger than kelp patches in our study region (Fig. 1C), transit times between kelp patches located within the same ROMS cell cannot be determined directly. To rectify this problem, we modeled the relationship between alongshore distance (measured between ROMS cell centroids) and mean oceanographic transit times (water-parcel connectivity) between all pairs of ROMS cells. To allow for asymmetrical transit times, we modeled upcoast and downcoast ROMS cell pairs separately. Locally weighted scatterplot smoothing (LOESS) indicated an asymptotic relationship, which we fit using a saturating function (transit time = $a \times$ alongshore distance / ($b +$ alongshore distance); $P < 0.001$; for upcoast pairs, $a = 71.8$, $b = 199.0$, $R^2 = 0.95$; for downcoast pairs, $a = 69.8$, $b = 129.7$, $R^2 = 0.89$). We then used this modeled relationship to predict asymmetrical oceanographic transit times for spores transported between all pairs of giant kelp patches as a function of the alongshore distances between patch centroids and the direction of transport.

ROMS solutions yielded transit times but did not account for the loss of kelp spores occurring during dispersal, such as mortality (pre- or post-settlement) or settlement at other patches between the source and recipient patches. Unfortunately, little is known about the loss rates of planktonic marine propagules, including kelp spores. In large aquaria designed to simulate a planktonic environment, Reed et al. (1992) found that half of giant kelp spores stopped swimming after 24 h and none swam beyond 120 h, possibly indicating exhaustion of energy stores (Brzezinski et al. 1993). For results presented here, we assumed a proportional spore loss rate of 0.9 d^{-1} ; however, we tested the sensitivity of our results to this assumption by varying proportional loss rates from 0.5 d^{-1} to 0.99 d^{-1} (see sensitivity analysis in Appendix A). Incorporating these loss rates with modeled oceanographic transport yielded effective spore dispersal distances (e.g., 50% probability of successfully dispersing 0.56 – 0.84 km and 1% proba-

bility of successfully dispersing 3.8 – 5.7 km) that were consistent with in situ measurements of giant kelp spore dispersal (Reed et al. 2004, Gaylord et al. 2006) and population genetics (Alberto et al. 2010, 2011).

Demographic connectivity estimates

Most estimates of demographic connectivity, especially in marine ecosystems, fail to explicitly consider patch-specific fecundities, which determine the numbers of dispersing individuals or propagules (Watson et al. 2010, Burgess et al. 2014). Landsat-derived estimates of giant kelp canopy biomass are a good predictor of local population fecundity (spore-bearing tissue density; Appendix B). Therefore, we used aggregate canopy biomass as a proxy for patch fecundity. We estimated relative demographic connectivity ($C_{j,t}$) of a population at patch j during semester t as

$$C_{j,t} = \frac{\sum_{i \neq j}^n b_{i,(t-0.5)}(1-l)^{d_{ij}}}{\max \left[\sum_{i \neq j}^n b_{i,(t-0.5)}(1-l)^{d_{ij}} \right]} \quad (1)$$

where $b_{i,(t-0.5)}$ is the canopy biomass of the population at patch i in the previous semester, l is daily proportional spore loss rate, and d_{ij} is the modeled transit time for spores dispersing from patch i to patch j (for n total patches in which $i \neq j$). We chose to predict local dynamics based on a single semester time lag in connectivity because giant kelp sporophytes generally take 6–9 months to mature to canopy-forming adults following spore settlement (Dayton et al. 1984). Our measure of relative connectivity was scaled by the maximum observed connectivity among all patches and semesters, and therefore was bounded between 0 and 1.

Statistical analyses

To determine the effects of connectivity and patch size on probabilities of local giant kelp occupancy, extinction, and colonization, we assessed the strength of evidence supporting multiple, a priori-specified generalized linear models (GLMs) and generalized linear mixed-effects models (GLMMs). All models used a logit link function to predict each binomial response variable as a function of relative connectivity (for each patch and semester) and patch size (i.e., the log of patch area, $\ln[\text{area}]$). We log-transformed patch area because theoretical and empirical metapopulation studies indicate that local population dynamics should respond to changes in patch size on a logarithmic scale (MacArthur and Wilson 1967, Hanski 1999, Reed et al. 2006a). For each response variable, we generated a set of five models (Table 1) by varying each of two random effects: semester and patch identity. Because of regional environmental stochasticity (e.g., El Niño Southern Oscillation [ENSO]), we expected certain semesters to be associated with greater or lesser likelihoods of local

TABLE 1. Model comparisons (Akaike statistics) for response variables (probabilities of local occupancy, extinction, and colonization) for patches of giant kelp (*Macrocystis pyrifera*) in southern California, USA, in a 22-yr metapopulation study. All models have two fixed effects (connectivity and patch size), and Model 1 has no random effects.

Model no.	Random effect(s)	k	Occupancy		Extinction		Colonization	
			Δ_i	w_i	Δ_i	w_i	Δ_i	w_i
1		3	2524.1	<0.001	761.2	<0.001	624.8	<0.001
2	Semester	4	1495.6	<0.001	141.7	<0.001	312.5	<0.001
3	Patch identity	4	1505.9	<0.001	704.2	<0.001	413.0	<0.001
4	Semester, patch identity	5	117.0	<0.001	33.7	<0.001	0	0.778
5	Semester (random slope), patch identity	7	0	>0.999	0	>0.999	2.5	0.222

Notes: The patch size term represents the log of patch area ($\ln[\text{area}]$). The number of model parameters is indicated by k . For each response variable, models with very strong support based on Akaike information criteria ($\Delta_i < 2$, where $\Delta_i = \text{AIC}_i - \text{AIC}_{\min}$ for model i) are shown in boldface. Akaike weight (w_i) is the probability that model i is best among all R candidate models, given the data. The proportional spore loss rate (l in Eq. 1) for these models was 0.9 d^{-1} , but all results were highly robust to variation in proportional spore loss rates ($l = 0.5\text{--}0.99 \text{ d}^{-1}$; see sensitivity analysis in Appendix A).

occupancy, extinction, and colonization (Edwards and Hernández-Carmona 2005, Parnell et al. 2010; Bell et al. 2015). We also anticipated that local population dynamics would vary spatially due to local environmental factors, such as exposure to wave disturbances, sea urchin grazing, or resource availability (Graham et al. 2007, Schiel and Foster 2015; Bell et al. 2015). Therefore, we included semester and patch identity as individual or crossed categorical random effects. Furthermore, we suspected that the relationship between relative connectivity and local population dynamics might differ among semesters due to, for example, temporal variation in oceanographic transport processes (Watson et al. 2010). To allow for this possibility, we specified models permitting the slope between connectivity and probabilities of occupancy, extinction, or colonization to vary randomly among semesters (all other GLMMs were random-intercept only models).

We analyzed models in R 3.1.2 (R Development Core Team 2014) using the package lme4, version 1.1-7 (Bates et al. 2014), and compared model parsimony using Akaike's information criterion (AIC) to optimize goodness of fit but avoid overfitting (Burnham and Anderson 2002). We estimated parameters and calculated AIC values by the maximum likelihood method (using the Laplace approximation for GLMMs; Bolker et al. 2009). We ranked models based on delta-AIC values (Δ_i), a measure of the strength of evidence of each model i relative to the best model (i.e., the model with the minimum AIC value; $\Delta_i = \text{AIC}_i - \text{AIC}_{\min}$). We considered $\Delta_i < 2$ to indicate substantial support for model i (Burnham and Anderson 2002). We report model comparisons as Δ_i and Akaike weights (w_i), the probability that model i is best among all R candidate models, given the data

$$w_i = e^{(-\Delta_i/2)} / \sum_{i=1}^R e^{(-\Delta_i/2)}. \quad (2)$$

Prior to all analyses, we standardized (converted to z scores) relative connectivity and patch size data so that we could directly compare their effects. For each response variable, we assessed multicollinearity between

fixed factors by measuring the variance inflation factor ($\text{VIF} = 1/[1 - R^2]$); in all cases multicollinearity was very low ($\text{VIF} < 1.15$). After selecting the most parsimonious model, we determined the significance of fixed factors by analysis of deviance via the Wald χ^2 test and performed model-based parametric bootstraps ($n = 1000$ simulations) to estimate 95% confidence intervals (CIs; Bolker et al. 2009).

RESULTS

Over the 22-yr (44-semester) time series, we observed 9589 occurrences/absences (in all 223 patches), 5997 extinction/persistence events (in 221 patches) of which 791 were extinctions (relative frequency = 0.132), and 3592 colonization/failure-of-colonization events (in 209 patches) of which 813 were colonizations (relative frequency = 0.226). The proportion of patches occupied and the numbers of extinctions and colonizations varied stochastically through time (Fig. 2). Mean durations of persistence and extinction were 4.0 ± 5.0 yr and 2.1 ± 3.3 yr, respectively; however, these estimates are conservative because persistence or extinction may have been ongoing beyond the range of the analyzed time series (i.e., prior to 1992 or after 2014). Over half of the persistence durations were ≤ 3 yr and over 70% of the extinction durations were ≤ 2 yr, with a long tail in both cases (Fig. 3), illustrating the highly dynamic nature of these populations and the suitability of our time series for testing the predictions from metapopulation theory.

The most parsimonious model explaining probabilities of occupancy and extinction was a GLMM incorporating crossed random effects (semester and patch identity) and a connectivity slope that varied randomly among semesters ($w_i > 0.999$; $\Delta_i \geq 117.0$ and $\Delta_i \geq 33.7$ for competing models of occupancy and extinction probabilities, respectively; Table 1). The probability of colonization was fairly well explained by an analogous model ($w_i = 0.222$; $\Delta_i = 2.5$; see model 5 in Table 1), but removing the random among-semester slope of connectivity improved model parsimony ($w_i = 0.778$; $\Delta_i = 0$; see model 4 in Table 1; $\Delta_i \geq 312.5$ for all other competing models), indicating that the relation-

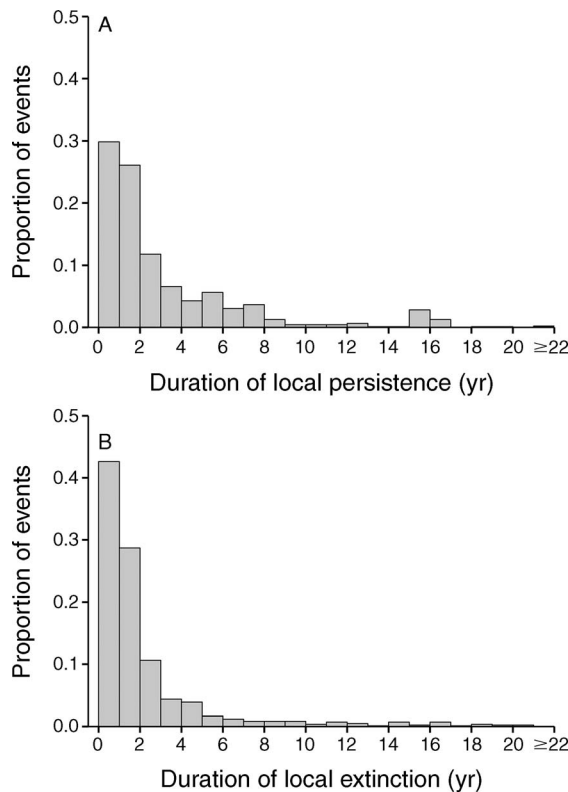


FIG. 3. (A) Frequency distribution of durations of (A) local persistence ($n = 958$ persistence periods in 221 patches) and (B) local extinction ($n = 847$ extinction periods in 209 patches) for giant kelp patches along the mainland coast of southern California, USA, from the second semester (July–December) of 1992 to the first semester (January–June) of 2014. Persistence and extinction durations represent the numbers of consecutive semesters (six-month periods) of giant kelp absence and presence, respectively.

ship between connectivity and the probability of colonization did not vary substantially through time. For all response variables, incorporating random effects of both semester and patch identity greatly improved

model parsimony ($\Delta_i \geq 141.7$ for less complex models; Table 1). Therefore, certain semesters and locations were associated with greater or lesser likelihoods of giant kelp occupancy, extinction, and colonization.

Demographic connectivity and patch size strongly predicted probabilities of local giant kelp occupancy, extinction, and colonization ($P \leq 0.002$; Table 2, Fig. 4). Increasing connectivity and patch size improved the probability of occupancy by giant kelp (Fig. 4A), reduced the probability of extinction (Fig. 4B), and enhanced the probability of colonization (Fig. 4C). Moreover, we did not observe any local extinctions when connectivity was over 0.31 (relative to the observed maximum; Fig. 4B).

The effect of connectivity on the probability of occupancy was essentially equivalent to that of patch size (Table 2; Fig. 4A). In contrast, connectivity had proportionally smaller effects on the probabilities of extinction and colonization relative to patch size (effect size for connectivity was 78% and 15% of patch size for the probabilities of extinction and colonization, respectively; Table 2, Fig. 4B, C). Unfortunately, however, our ability to examine how connectivity affected colonization was limited because we did not observe any colonization or failure-of-colonization events for patches with relative connectivity over 0.69 (Fig. 4C).

As patch size increased, the positive impact of connectivity on occupancy, extinction, and colonization tended to diminish (Fig. 4). Connectivity strongly improved probabilities of occupancy and persistence for small and moderately sized patches, whereas extinction was highly unlikely ($<5\%$) in very large patches ($>\sim 32$ ha) regardless of connectivity (Fig. 4A, B). The probability of colonization, on the other hand, was highly sensitive to connectivity across a broad range of patch sizes (Fig. 4C).

All results were highly robust to variation in proportional spore loss rates ($l = 0.5\text{--}0.99 \text{ d}^{-1}$; see sensitivity analysis in Appendix A).

TABLE 2. Results of the analysis of deviance for each fixed factor in the most parsimonious model (see Table 1) by the Wald χ^2 test.

Response variable and fixed factor	Standardized effect size (95% CI)	χ^2 df	Likelihood ratio χ^2	$P (>\chi^2)$
Probability of occupancy				
Connectivity	1.77 (1.36–2.25)	1	53.17	<0.001
Patch size	1.78 (1.56–2.03)	1	246.89	<0.001
Probability of extinction				
Connectivity	0.90 (0.51–1.35)	1	16.21	<0.001
Patch size	1.15 (1.00–1.30)	1	225.73	<0.001
Probability of colonization				
Connectivity	0.18 (0.06–0.32)	1	9.16	0.002
Patch size	1.19 (0.98–1.43)	1	99.85	<0.001

Notes: The patch size term represents the log of patch area ($\ln[\text{area}]$). The proportional spore loss rate (l in Eq. 1) for these models was 0.9 d^{-1} , but all results were highly robust to variation in proportional spore loss rates ($l = 0.5\text{--}0.99 \text{ d}^{-1}$; see sensitivity analysis in Appendix A). We estimated 95% confidence intervals (CIs) for standardized effect sizes using model-based parametric bootstraps ($n = 1000$ simulations).

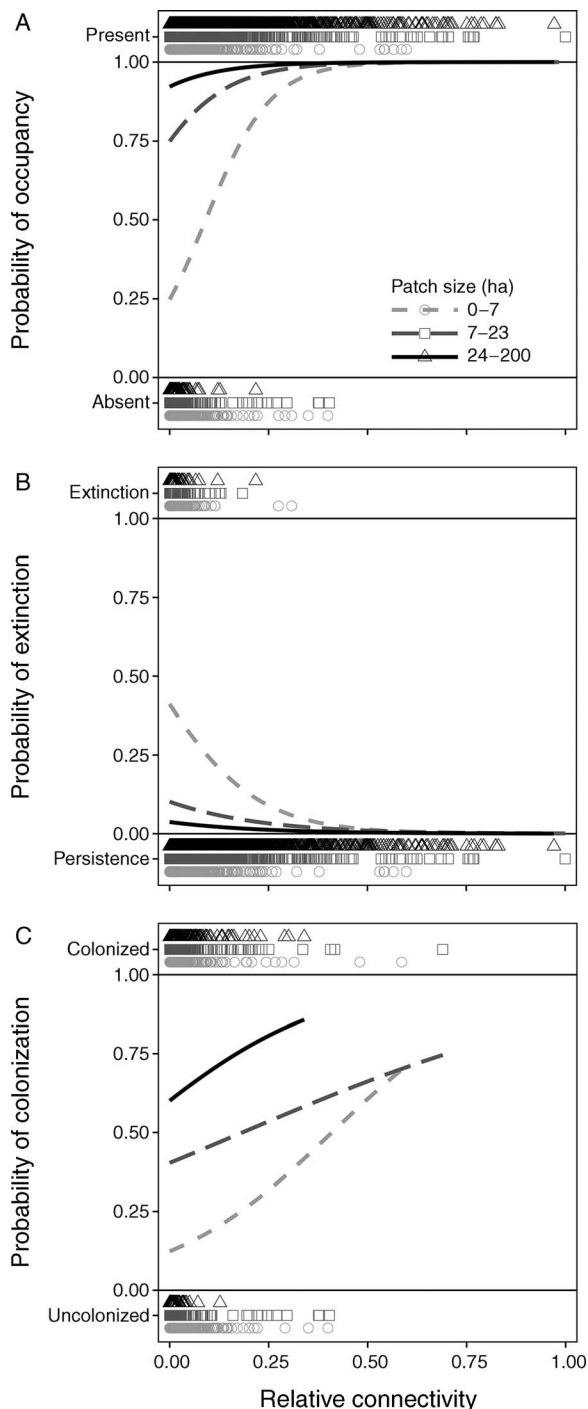


FIG. 4. Probabilities of local giant kelp (A) occupancy in a given semester (six-month period), and (B) extinction and (C) colonization events between consecutive semesters as a function of connectivity and patch size. Symbols above and below the main panels indicate actual data. Curves are logistic regressions based on model predictions for fixed effects only (i.e., excluding random effects and their uncertainties). Different symbols (data) and line types (predictions) indicate patch size subdivided into quantiles (33% equal-frequency area bins). The proportional spore loss rate (l in Eq. 1) for these model predictions was 0.9 d^{-1} , but all results were highly robust to variation in proportional spore loss rates ($l = 0.5\text{--}0.99 \text{ d}^{-1}$; see sensitivity analysis in Appendix A).

DISCUSSION

Our results demonstrate that demographic connectivity among patches can strongly determine local population dynamics. Increasing connectivity enhanced the likelihood of giant kelp occupancy by reducing the probability of extinction and improving the probability of colonization. However, patch size also influenced local dynamics and mediated the effect of connectivity. Moreover, the relationship between connectivity and local population dynamics varied over time, possibly due to temporal variation in oceanographic transport processes. Connectivity and patch size had approximately equivalent effects on occupancy and extinction probabilities but, surprisingly, connectivity had a relatively smaller influence on the likelihood of colonization, perhaps due to local ecological processes that differ between extinct and extant patches.

Our analysis constitutes one of the longest (22 years, or up to 22 generations, assuming annual recruitment; Graham et al. 2007) and largest ($\sim 500 \text{ km}$, or at least 2 orders of magnitude larger than average dispersal distances; Gaylord et al. 2006, Alberto et al. 2010) empirical tests of metapopulation theory (Hanski 1999, Ojanen et al. 2013), especially among studies in marine ecosystems (López-Duarte et al. 2012, Burgess et al. 2014) or of plants and algae (Ouborg and Eriksson 2004, Reed et al. 2006a). Our unique population survey represents a census, not a sample, of local populations within the study region and avoids common simplifying assumptions of population abundance (Eaton et al. 2014). Furthermore, our novel patch delineation approach surmounts the mega-patch problem (Cavanaugh et al. 2014). Our connectivity metric incorporates advective transport processes and fecundity (as estimated from biomass) of source populations, which are both typically overlooked in metapopulation studies (Watson et al. 2010, Burgess et al. 2014). Our demonstration of the importance of demographic connectivity to local population dynamics represents the first comprehensive evidence that southern California giant kelp populations function as a metapopulation system, confirming earlier hypotheses (Reed et al. 2006a) and challenging the common view that populations of this key foundation species are governed exclusively by self-replenishment (reviewed in Graham et al. 2007).

Local population extinction

Connectivity may have reduced the semesterly probability of local extinction by increasing overall population growth (Pulliam 1988) or buffering against stochastic events (Stacey and Taper 1992), such as wave disturbance, nutrient stress, or herbivory, which can denude even large patches (Schiel and Foster 2015). A third possibility is that connectivity improved local genetic variation and reduced inbreeding depression (Saccheri et al. 1998), which can suppress giant kelp reproduction and survival (Raimondi et al. 2004). Future studies that track giant kelp abundance at

smaller spatial scales (e.g., individuals or clusters of individuals) may identify important intra-patch population dynamics and shed light on the mechanistic links between connectivity and persistence, such as the potential for rescue effects (Pulliam 1988).

Patch size influenced probabilities of local occupancy and extinction of giant kelp, with an effect size similar to connectivity. Bigger patches have the potential to support larger populations and therefore are generally more resilient to environmental stochasticity (MacArthur and Wilson 1967, Hanski 1999). As expected based on theory, patch size mediated the effect of connectivity on local population dynamics (Fig. 4). Connectivity had a large effect on the probability of extinction for small (0–7 ha) and moderate (7–23 ha) sized patches, but this effect diminished with increasing patch size. The probability of persisting to the next semester saturated near 1 (i.e., no risk of extinction) for very large (>24 ha) patches regardless of the degree of connectivity, while the smallest (<1 ha) patches had less than a 50% chance of persisting to the next semester even under the highest connectivity.

Colonization following local extinction

Connectivity also played a key role in patch colonization following local extinction, indicating the importance of connectivity for recolonization (MacArthur and Wilson 1967) and corroborating previous empirical studies (Hanski 1999). Most extinction periods were short (≤ 2 years), matching earlier observations of rapid giant kelp recovery following local extinction (Reed et al. 2006a). However, some patches failed to be colonized for many years and a few were extinct for nearly the entire 22 years of our investigation (Fig. 3B). Our results indicate that highly isolated patches face lower semesterly probabilities of colonization (Fig. 4C). Because giant kelp spores typically disperse only meters to a few kilometers (Gaylord et al. 2006, Alberto et al. 2010), it is not surprising that some very isolated patches take a long time to recover following extinction. For these patches, chance spore transport events associated with rare ocean circulation patterns (Watson et al. 2010) or long-distance dispersal of dislodged, fecund kelp (Hernández-Carmona et al. 2006) may be crucial to colonization. If self-fertilization reduces the fitness of isolated kelp populations through inbreeding depression (Raimondi et al. 2004), occasional colonization from other populations may be even more critical to the long-term persistence of isolated populations (Saccheri et al. 1998).

Connectivity was less predictive of the probability of colonization than it was for the probabilities of occupancy or extinction, especially when compared to the consistent effect of patch size (Table 2, Fig. 4). There are several pre- and post-settlement processes that differ between extinct and extant patches that could play a role in disrupting the link between connectivity and colonization. For example, denuded reefs are often associated

with higher densities of sea urchins, which can greatly reduce the survival of juvenile giant kelp (Dayton et al. 1984, Harrold and Reed 1985). Patches lacking giant kelp are also more likely to support an abundance of understory macroalgae (Dayton et al. 1984) that can outcompete early life-history stages of giant kelp (Reed and Foster 1984, Reed 1990). Storms that cause local giant kelp extinction can also transport sediments over low-relief reefs, reducing effective patch size and inhibiting recruitment success (Geange et al. 2014), sometimes for many years (Reed et al. 2008).

Factors affecting spore settlement and recruitment may also play a role in decoupling connectivity and colonization, but their influences are poorly understood. Spore settlement may differ between extinct and extant patches because giant kelp fronds attenuate water flow and turbulence (Gaylord et al. 2007). However, due to the complexities of local hydrodynamics, it is unclear whether kelp forests facilitate or inhibit spore settlement (Gaylord et al. 2006). Additionally, male and female giant kelp spores must settle at high densities to ensure fertilization (>1 spore/mm²; Reed 1990). Because spore supply is coupled to local abundance (Appendix B), spores settling within extinct patches may be unlikely to encounter the high spore densities necessary for fertilization. Lastly, early life-history stages of giant kelp (gametophytes and microscopic sporophytes) are capable of arrested development (up to a few months; Edwards and Hernández-Carmona 2005) and this could further disrupt the relationship between connectivity and colonization. However, additional research is needed to evaluate the survival and demographic importance of latent early life-history stages (Carney et al. 2013).

Increasing patch size enhanced the probability of patch colonization (Fig. 4C). We speculate that bigger patches offer a larger target area for spore settlement, as well as greater within-patch environmental heterogeneity that may promote the likelihood of successful settlement and recruitment. Our results offer support for earlier studies predicting that patch size alters the probability of colonization (MacArthur and Wilson 1967, Eaton et al. 2014) and suggest caution to spatially realistic metapopulation models that assume colonization rates are independent of patch size (Hanski 1999).

Spatiotemporal variation in environmental conditions and connectivity

Probabilities of giant kelp occupancy, extinction, and colonization varied over space and time. It is well documented that patches in certain locations face different likelihoods of giant kelp mortality due to wave exposure, grazing by sea urchins, or availability of nutrients or light (Graham et al. 2007, Schiel and Foster 2015, Bell et al. 2015). Regional environmental conditions vary seasonally and interannually (e.g., ENSO), and this can mediate giant kelp loss and recovery

(Edwards and Hernández-Carmona 2005, Parnell et al. 2010; Bell et al. 2015). Furthermore, although the production and release of giant kelp spores occur year-round, they tend to be most pronounced during the winter and spring (Reed et al. 1996, 1997). Therefore, spatiotemporal variation in environmental conditions plays an important role in governing local population dynamics and may mediate the degree and consequences of connectivity.

Oceanographic transport processes also vary over space and time and likely have a strong influence on connectivity (Reed et al. 2006a). Our oceanographically based spore dispersal estimates account for known spatial, seasonal, and interannual variations in regional ocean circulation and hence are likely more accurate than phenomenological or Euclidian-distance models (Gaylord et al. 2006, Mitarai et al. 2009, Alberto et al. 2010). In particular, our approach allows for asymmetrical connectivity, a process especially important to metapopulation dynamics when dispersal is dominated by physical advection (e.g., wind dispersal of seeds, oceanic transport of planktonic propagules) but typically overlooked in metapopulation models (Ouborg and Eriksson 2004, Watson et al. 2010, Kleinhans and Jonsson 2011). Because ROMS ocean circulation solutions were only available for about half of the giant kelp biomass time series (1996–2007), we estimated spore dispersal using average oceanographic transit patterns and allowed the relationship between connectivity and local population dynamics to vary among semesters. As anticipated, this type of random-effect structure greatly improved model fit, indicating that the importance of connectivity to local population dynamics varies over time. Future studies that realistically model seasonal and interannual variation in both propagule production and dispersal are likely to provide additional insight into the role of temporal dispersal variation in metapopulation dynamics.

Spatial synchrony, connectivity, and local population dynamics

Together with previous studies (Reed et al. 2006a, Cavanaugh et al. 2013), our findings suggest that connectivity among local populations is likely an important but overlooked cause of synchrony in the southern California giant kelp metapopulation system. In this region, giant kelp spore dispersal does not appear to be substantial enough to result in panmixia (Alberto et al. 2010), broad synchrony (Cavanaugh et al. 2013), and elevated risks of simultaneous local extinctions. Although adjacent, well-connected local populations are highly synchronous (Cavanaugh et al. 2013), we found no evidence that they had higher extinction probabilities (Fig. 4B). Further work is needed to clarify the relative roles of and possible interactions among different synchronizing mechanisms (e.g., propagule production, dispersal, environmental conditions, herbivory; Heino et al. 1997, Reed et al. 1997, Watson et al. 2010) in giant

kelp population dynamics, as well as to search for the existence of synchronous sub-networks within the southern California metapopulation system (Cavanaugh et al. 2013).

Implications for management and conservation

Giant kelp forests increase biodiversity, alter biogeochemical cycles, enhance fisheries yields, stimulate recreation and tourism, provide cultural value, and, in some regions, support economies through kelp harvest (Graham et al. 2007, Schiel and Foster 2015). Because these ecosystem services are generally utilized and managed locally, knowledge of how connectivity affects the local dynamics of giant kelp is of concern for natural resource stakeholders, managers, policymakers, and conservation groups. Our results indicate that demographic connectivity is a key factor not only to the colonization of denuded reefs but also to the persistence of extant kelp forests. These findings counter the common view that giant kelp populations are replenished solely by locally produced spores and regulated without interactions among local populations (reviewed in Graham et al. 2007). A better understanding of the factors regulating local populations, such as spatiotemporal variation in propagule production and dispersal, or interactions between connectivity and local ecological factors (e.g., herbivory, competition, disturbance), should improve the management of giant kelp forests under altered disturbance regimes, the mitigation of giant kelp loss (e.g., from pollution; Reed et al. 2006b), and the restoration of degraded giant kelp habitats (North 1976).

Future studies should also aim to understand how local giant kelp populations and interactions among them influence the structure and function of the broader metapopulation system. Local populations likely vary greatly in their importance to network-scale dynamics (e.g., by functioning as persistent sources of propagules or as critical demographic links among clusters of patches) and future work should ascertain which patches have particularly prominent conservation value (Watson et al. 2011). Many species, including several with high economic and conservation value, rely on giant kelp for food or habitat, and giant kelp forests strongly alter species interactions and community structure (Graham et al. 2007, Schiel and Foster 2015). Therefore, the southern California metapopulation system may form the foundation of a giant kelp forest metacommunity system (Leibold et al. 2004), an interesting possibility that has received few empirical tests (Guichard et al. 2004, White and Caselle 2008). Applying a metacommunity framework to giant kelp forests may enhance regional multispecies management and conservation actions, such as the restoration of exploited species (Lipcius et al. 2008) and the design of marine protected area networks (Guichard et al. 2004, Watson et al. 2011, Burgess et al. 2014).

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SUPPLEMENTAL MATERIAL

Ecological Archives

Appendices A and B are available online: <http://dx.doi.org/10.1890/15-0283.1.sm>