Regeneration and expansion of *Quercus tomentella* (island oak) groves on Santa Rosa Island

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ABSTRACT.—*Quercus tomentella* (island oak) is an endemic species that plays a key functional role in Channel Island ecosystems. Growing in groves on highland ridges, *Q. tomentella* captures fog and increases water inputs, stabilizes soils, and provides habitat for flora and fauna. This cloud forest system has been impacted by a long history of ranching, and restoration efforts are underway that include erosion control, leaf litter capture, fog capture, and reforestation. To inform restoration efforts, we explored tree regeneration and the potential for *Q. tomentella* grove expansion on Santa Rosa Island. We delineated current and historic groves at Black Mountain by comparing stand maps from 1989 and aerial photographs from 1994 and 2015. We evaluated regeneration in the outlying areas by recording the location, diameter at breast height, number of trunks, height class, percent crown mortality, nurse plant species (if present), and reproductive status for all 4355 outlying seedlings, saplings, and mature trees. We defined outliers as individuals that were 15 m outside of the canopy of island oak groves. There are 14 groves at Black Mountain, and grove size expanded by an average of 36.9% (SD 18.5%) between 1994 and 2015. Nurse plants correlated positively with outlier tree height and reduced percent crown mortality. This effect is potentially due to increased fog drip from nurse plant species such as *Quercus pacifica* (island scrub oak), *Heteromeles arbutifolia* (toyon), and *Baccharis pilularis* (coyote brush). These results indicate that *Q. tomentella* is regenerating and that nurse plants can serve as catalysts for ecosystem restoration.

RESUMEN.—El *Quercus tomentella* (encino de la isla) es una especie endémica que desempeña un papel funcional clave en los ecosistemas de las Islas del Canal (Channel Islands). El *Q. tomentella*, que crece en las arboledas de las cordilleras montañosas, captura la niebla, aumenta el aporte de agua, estabiliza los suelos y proporciona un hábitat para la flora y la fauna. Este sistema de bosque de niebla ha sido afectado por una larga historia de ganadería, por lo que se están llevando a cabo labores de restauración que incluyen control de la erosión, recogimiento de hojarasca, captura de niebla y reforestación. Para proporcionar un informe de las labores de restauración, estudiamos la regeneración de los árboles y el potencial de expansión de los bosques de *Q. tomentella* en la Isla Santa Rosa. Demarcamos los bosques actuales y los históricos en Black Mountain comparando mapas forestales de 1989 con fotografías aéreas de 1994 y 2015. Evaluamos la regeneración en las áreas periféricas registrando la ubicación, el diámetro a la altura del pecho, el número de troncos, el tipo de altura, el porcentaje de mortalidad de las copas, las especies de plantas nodrizas (si las hubiere) y el estado reproductivo de las 4355 plántulas periféricas, retoños y árboles maduros. Definimos como individuos atípicos a aquellos encinos que se encontraron a 15 m por arriba del dosel de los robledales de la isla. Existen 14 arboledas en Black Mountain, las cuales se expandieron en un promedio de 36.9% $\pm$ 18.5% entre 1994 y 2015. Las plantas nodrizas se correlacionaron positivamente con la altura de los árboles atípicos y con un reducido porcentaje de mortalidad de las copas. El efecto de las especies nodrizas podría deberse al aumento del goteo de niebla de especies tales como el *Quercus pacifica* (roble de matorral insular), la *Heteromeles arbutifolia* (baya de navidad) y el *Baccharis pilularis* (arbusto coyote). Estos resultados indican que el *Q. tomentella* se está regenerando y que las plantas nodrizas pueden servir como catalizadores en la restauración del ecosistema.

Oaks play a key functional role in many global woodland communities, and many oak species are in decline (Costa et al. 2011). One such species is *Quercus tomentella* (island oak), which grows on highland ridges in the Channel Islands of California (Fig. 1). *Quercus*

tomentella is a narrow endemic species listed as vulnerable by the International Union for the Conservation of Nature (IUCN) and of limited distribution by the California Native Plant Society (CNPS) (IUCN 2015, CNPS 2015). A history of intensive ranching at the

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Fig. 1. Project location in Channel Islands National Park, California.

Channel Islands impacted *Q. tomentella* groves, and their regeneration may now be hindered by reduced fog drip, soil loss, and lack of seedling establishment and survival.

Quercus tomentella captures water from fog to create moist cloud forest conditions below canopy driplines, where the abundant leaf litter (up to 60 cm deep) promotes infiltration and maintains soil moisture (Fig. 2) (Kindsvater 2006, Williams et al. 2008, Schumann et al. 2014). Fog drip has been observed in pines, oaks, and shrubs across the Channel Islands (Williams et al. 2008, Fischer et al. 2009, Evola and Sandquist 2010, Wang et al. 2017). Fog drip contributes to groundwater recharge to maintain downslope springs and stream base flow (Stock et al. 2003, Sawaske and Freyberg 2015, Rastogi et al. 2016, Wang et al. 2017). *Quercus tomentella* groves also provide habitat for ecologically important island vertebrate and invertebrate species (Koenig and Stahl 2007, Puerta-Piñero et al. 2010, Sanchez and Hudgens 2015).

There has been a progressive loss of pine and oak woodlands on the highland ridges

due to the long history of sheep and cattle ranching at the Channel Islands (Allen 1996). Acorn predation by rooting feral pigs disturbed root systems and impacted oak regeneration (Barrios-Garcia and Ballari 2012). Reduced vegetative cover and disturbance to biological soil crusts also induced widespread gully erosion and landslides in the highlands (Brumbaugh et al. 1982, Renwick 1982, Van Vuren and Coblenz 1987, Klinger et al. 2002, Pinter and Vestal 2005, Perroy et al. 2012). Many ridgelines were denuded down to the exposed bedrock or regolith (Fig. 2).

Like other California oaks, the regeneration success of *Q. tomentella* following disturbance is unclear (Smith 1993, McCreary 2001). The potential mechanisms of island oak regeneration are via cloning and seed dispersal by gravity, birds, and mammals. Clones develop from root sprouts emerging through the soil and leaf litter to expand the canopy extent as trees reach maturity (Liñán et al. 2011). Acorns fall off trees, roll downhill and then germinate (Matsuda et al. 1989). Birds may also contribute to dispersion by foraging in the

Fig. 2. Representative photos of *Quercus tomentella* on Santa Rosa Island: **A**, fog bank in the lower reaches of the watershed below Black Mountain; **B**, acorn germination in leaf litter; **C**, fog drip occurring in a grove at Black Mountain; **D**, bare and denuded ridgeline on Soledad Peak where temperature, moisture, and nutrient levels are adverse to germinating seedlings. The few surviving *Q. tomentella* trees on Soledad Peak have exposed roots, indicating extensive topsoil loss.

groves and relocating acorns to nests, caches, or other germination locations. However, unlike on Santa Cruz Island, there are no *Aphelocoma insularis* (Island Scrub Jay) individuals to disperse island oak seeds through lost caches on Santa Rosa Island (SRI) (Atwood 1980, Kindsvater 2006, Pesendorfer et al. 2014, Morán-López et al. 2015). Seed-eating rodents that forage in island oak groves may also cache acorns in burrows, which can lead to germination and stand growth (Li and Zhang 2003, Puerta-Piñero et al. 2010). Rodent dispersion is confined to the endemic island deer mouse (*Peromyscus maniculatus santarosae*), which is the only rodent on SRI.

Following establishment of Channel Islands National Park in 1980, ecosystem restoration efforts were initiated to address resource degradation. The first phase was passive restoration following the removal of all nonnative ungulates, and the resulting changes were dramatic. Woody vegetation types increased and grassland and bare ground cover decreased over time (Klinger et al. 2002, Corry and McEachern 2009, Beltran et al. 2014, Rick et al. 2014, Summers et al. 2018). The current active restoration phase consists of erosion control, leaf litter capture, and fog

capture to build soil resources and prepare for island oak and bishop pine (*Pinus muricata*) reforestation in the highlands (Kindsvater 2006, Klemm et al. 2012).

There is a need to better understand *Q. tomentella* regeneration to improve restoration efforts at the Channel Islands. In this study, we present preliminary results of an ongoing study of *Q. tomentella* regeneration at Santa Rosa Island (SRI). The study was conducted at 14 groves at Black Mountain. We evaluated changes in grove size over time and mapped tree regeneration in the outlying areas. We also investigated the effect of nurse plants such as *Heteromeles arbutifolia* (toyon), *Baccharis pilularis* (coyote brush), *Adenostoma fasciculatum* var. *prostratum* (prostrate chamise), and *Arctostaphylos confertiflora* (Santa Rosa Island manzanita) on island oak stem diameter, height, and health. Nurse plants may increase regeneration health and vigor due to increased soil moisture from fog drip.

STUDY AREA

Santa Rosa Island is the second largest island (215.3 km²) in Channel Islands National Park and is located 42 km off the coast of

California (Fig. 1). The rugged terrain is dominated by east–west trending ridgelines with deep canyons, with the highest peak at 482.5 m above sea level. The island has a maritime Mediterranean climate, precipitation mostly occurs between October and April, and summer fog drip contributes significant moisture to ecosystems. Strong prevailing north-west winds can deplete soil moisture and cause wind erosion on denuded ridgelines. Vegetation comprises valley and foothill grassland, riparian areas, coastal scrub (coyote brush scrub, coastal sage scrub, lupine scrub, caliche scrub, and coastal bluff scrub), island chaparral, and woodlands (oak, mixed, and island pine woodlands) (Clark et al. 1990). Among the tree species found on the island, 4 are rare and ecologically important: *Q. tomentella*, *Pinus torreyana* ssp. *insularis* (Santa Rosa Island Torrey pine), *P. muricata*, and *Lyonothamnus floribundus* ssp. *aspleniifolius* (island ironwood). *Quercus tomentella* is located predominantly in 2 areas of SRI, on Black Mountain and the Soledad Ridge.

Land use on SRI dates back 13,000 years to the Island Chumash. Ranching was introduced in 1843, with herd sizes of approximately 100,000 sheep and 5000 cattle by the early 1900s (Livingston 2006). Channel Islands National Park was created in 1980, and Santa Rosa was purchased and incorporated into the park in 1986. Animal removal began shortly thereafter. All feral pigs were eradicated by 1992, cattle were removed in 1998, and deer and elk were systematically culled and removed by the end of 2011 (McEachern et al. 2016). Based on analysis of Landsat TM5 and ETM+ satellite imagery from 1989 to 2015, scrub cover increased by 41%, island chaparral increased by 14%, and woodland cover increased by 109%. In contrast, valley and foothill grassland cover decreased by 31% and bare ground by 68% (Summers et al. 2018). Despite evidence of recovery following non-native grazer removal, approximately 5.6 km² of the island remains bare and may require more active intervention.

The study site is located off Soledad Road on Black Mountain, approximately 6.4 km west of Bechers Bay pier and the CSUCI Santa Rosa Island Research Station. The site starts 0.44 km east of the weather station at the first *Q. tomentella* on the hillside adjacent to Soledad Road, and extends 1.04 km west to

the last *Q. tomentella* on this hillside. The study area is a predominantly north-facing slope.

METHODS

We used a combination of field and geospatial methods to evaluate current and historic *Q. tomentella* grove size and map the current distribution of outlier trees on Black Mountain. We set up a perimeter for each of the current groves by taking a GPS waypoint at the stem of every adult *Q. tomentella* located at the edge of the groves. We defined a grove as a semicontinuous canopy cover with <15-m gaps between adult island oak driplines. Adult and juvenile trees with ≥15-m gaps from the main grove were considered outlier trees. The waypoints identifying the trees at the edge of each grove allowed us to identify the edge of island oak groves and differentiate *Q. tomentella* from *Q. pacifica* and *H. arbutifolia* in both current and historic aerial photographs. We delineated all groves and their canopy lines at Black Mountain by interpreting aerial photos from 4 January 2015 in Google Earth™, using the GPS waypoints at the grove edges to guide the polygon delineation.

The objective of the study was to compare the current (2015) *Q. tomentella* groves and outlier trees on Black Mountain with a historic grove map digitized from a 1:250,000 topographic map created in 1989 (Kindsvater 2006). In addition to investigating the 1989 map, we delineated the historic *Q. tomentella* groves by interpreting aerial photos from 2 September 1994 in Google Earth™. We used the 1989 grove polygons and GPS waypoints established at the adult trees at edges of the *Q. tomentella* groves to guide the historic grove delineation. The mature trees were assumed to still be alive and present in the 1994 aerial photos. Using this process, we generated polygons suitable for comparison to the 2015 grove delineations.

All grove polygons were imported to a GIS environment and projected in North American Datum 1983, Universal Transverse Mercator Zone 11N (NAD 83, UTM Zone 11N), the same projection as used for the GPS waypoints of the outlier trees. We calculated grove size in hectares for 1994 and 2015 and calculated the total change and the percent change over time. We determined whether grove size has changed significantly between

TABLE 1. Height classifications for *Quercus tomentella* outlier trees.

Height classification	Height range (cm)	Height median (cm)
1	<30	15
2	30–160	95
3	161–300	230
4	301–600	450
5	>600	700

1994 and 2015 by using a paired sample Student's *t* test.

We searched the exterior of the groves for outlying seedlings, saplings, and adult trees (outlier trees) and collected a waypoint at each outlier tree. We defined seedlings as stems ≤ 0.1 cm DBH (diameter at breast height), saplings as stems between 0.2 and 5 cm DBH, and adults as stems > 5 cm DBH. Note that we were not able to differentiate between stems established by seed germination from stems established as root suckers (clones) without digging to observe root systems. For each stem we recorded DBH, number of trunks, height class (Table 1), percent crown mortality (5% intervals), nurse plant species (if present), and reproductive status (yes/no). Reproductive status was determined by a visual scan for acorns growing on the tree. We defined a nurse plant as a tree or shrub that had a dripline that overlapped with a *Q. tomentella* seedling or the trunk, roots, or canopy of a sapling and therefore could provide water via fog drip. Adult outlier *Q. tomentella* trees were also considered nurse plants if oak seedlings or saplings were growing beneath them. For steep slopes where it was unsafe to collect data, we calculated the coordinates of outlier trees by measuring cardinal direction and distance from a Rangefinder™ placed at a known location. Binoculars were used to estimate DBH, number of trunks, and height class of outliers on steep and inaccessible slopes. We also made natural history observations about dispersal and patterns of tree regeneration.

We tested the correlations between nurse plant species and outlier tree DBH, height class, and percent crown mortality with a Browne–Forsythe ANOVA assuming unequal variance and a Games–Howell post hoc comparison of means, a robust test for nonnormally distributed data. We excluded 15.3% of the outlier trees from this analysis, as we

excluded outlier trees that were estimated with a Rangefinder™ and outlier trees that were also considered adult nurse trees.

RESULTS

There are 14 island oak groves at Black Mountain, and these ranged from 0.1 to 1.6 ha in size in 2015. All groves expanded 36.9% (SD 18.5%) on average ($P = 0.029$) from 1994 to 2015 (Fig. 3). The smallest grove expansion was 8.1% and the largest grove expansion was 78.5%.

We mapped 4355 *Q. tomentella* outlier trees on Black Mountain (Fig. 4). The majority of outlier trees are seedlings or saplings, with adult outlier trees making up only 12.2% (Fig. 5). The majority of the adult trees were visible in both the 1994 and 2015 aerial photos. While the majority of outlier trees are clustered around existing groves, outlier seedlings and saplings are widely distributed. Many were found > 200 m from existing groves or adult trees and/or dispersed across geographic barriers such as ravines and ridgelines. A total of 39.3% of the outlier trees had nurse plants (Table 2). The most common nurse plants were *Q. tomentella* (37.0%) and *B. pilularis* (30.8%), with *Q. pacifica* (15.5%), *A. fasciculatum* (11.3%), *A. confertifolia* (2.4%), and *H. arbutifolia* (1.8%) less commonly observed as nurse plants.

There was a statistically significant increase in outlier tree height if a *Q. tomentella*, *B. pilularis*, *Q. pacifica*, or *H. arbutifolia* nurse plant was present, compared to outlier trees with no nurse plant (Table 2). However, there was no difference in outlier tree height if an *A. fasciculatum* or *A. confertifolium* nurse plant was present. There was also a statistically significant decrease in percent crown mortality if a *Q. tomentella* or *H. arbutifolia* nurse plant was present, compared to outlier trees with no nurse plant (Table 2). However, there was no difference in percent crown mortality if a *B. pilularis*, *Q. pacifica*, *A. fasciculatum*, or *C. confertifolia* nurse plant was present. There was no difference between the DBH of outlier trees with nurse plants and outlier trees with no nurse plants (Table 2).

We found 3 *Peromyscus maniculatus* (deer mouse) acorn caches; however, only the exterior of the acorns were present and the seeds were not viable. The *P. maniculatus* caches were located in sandy caverns, indicating that the

Fig. 3. Comparison of the 1994 and 2015 *Quercus tomentella* groves at Black Mountain, Santa Rosa Island.

acorns were eaten in a safe location rather than stashed for future use. We found 2 sites with dead branches stuffed with acorns, providing evidence of *Melanerpes formicivorus* (Acorn Woodpecker) activity on Black Mountain. However, none of these acorns were viable. *Pipilo maculatus* (Spotted Towhee) individuals were seen kicking acorns downhill while foraging, and no *Corvus corax* (Common Raven) individuals were sighted with acorns.

DISCUSSION

Quercus tomentella groves have expanded from 1994 to 2015. Downslope expansion and infill from regeneration or cloning appears to be occurring across all groves. This contrasts with many oak species (e.g., *Q. douglasii* [blue oak], *Q. lobata* [valley oak], and *Q. suber* [cork oak]) in Mediterranean climates, where regeneration is sparse and patchy and species are in overall decline (Smith 1993, McCreary 2001, Pausas et al. 2009). Given the spatial distribution of the 4355 outlier trees, it is likely that *Q. tomentella* groves at Black Mountain will

continue to expand as seedlings mature and form additional canopy. The abundance of seedlings and saplings compared to adult trees indicates that regeneration and grove expansion may be a recent phenomenon following nonnative grazer removal. The extent and spatial distribution of grove expansion will be influenced by tree survival over time.

Despite the abundance of outlier trees, there are very few seedlings and saplings inside the groves except under canopy gaps where sunlight can reach the forest floor. In 2003–2004, Kindsvater (2006) sampled 14 plots ranging from 208 to 220 m² within *Q. tomentella* stands and found that 6 of the 14 stands had seedlings (plants <2.5 cm in stem diameter) ranging in number from 1 to 27, while saplings (plants 2.5 to 8 cm in stem diameter) were not present in any plot. Kindsvater attributed this size-class pattern to decreased herbivory associated with the removal of feral animals from the island that allowed some seedlings to survive in recent years.

Nurse plants positively affected the growth of *Q. tomentella* regeneration, increasing tree

Fig. 4. The locations of the 4355 *Quercus tomentella* outlier seedlings, saplings, and adult trees in comparison to 14 groves mapped in 2015 at Black Mountain, Santa Rosa Island. Based on field observation and terrain analysis, regeneration is mostly occurring downslope of the existing canopy edges.

Fig. 5. Stem size class distribution of the outlier trees at Black Mountain, Santa Rosa Island.

TABLE 2. The effect of nurse plant species on diameter at breast height (DBH), height, and crown mortality of *Quercus tomentella* outlier trees. Means are given with standard error in parentheses. Statistical significance was tested with a Browne–Forsythe ANOVA assuming unequal variance and a Games–Howell post hoc comparison of means.

Nurse plant	N	DBH (cm)	Height (cm)	% Mortality
<i>Quercus tomentella</i>	536	2.9 (0.2)	240.3 (6.6)*	8.8 (0.5)*
<i>Baccharis pilularis</i>	446	3.1 (0.2)	270.1 (6.1)*	10.2 (0.7)
<i>Quercus pacifica</i>	224	2.8 (0.3)	251.2 (8.5)*	9.8 (0.8)
<i>Adenostoma fasciculatum</i> var. <i>prostratum</i>	163	2.0 (0.5)	190.5 (10.8)	11.0 (1.2)
<i>Arctostaphylos confertifolia</i>	34	1.9 (0.4)	226.9 (22.9)	9.6 (5.5)
<i>Heteromeles arbutifolia</i>	25	4.7 (1.1)	317.1 (21.1)*	7.0 (1.0)*
No nurse plant	2241	2.6 (0.1)	211.0 (3.3)	12.0 (0.3)

*The mean difference is significant ($P < 0.01$) based on a Browne–Forsythe ANOVA assuming unequal variance. Statistical significance was calculated based on a comparison of outlier trees with nurse plants and outlier trees with no nurse plant using a Games–Howell post hoc comparison of means.

height and decreasing crown mortality. The most effective nurse species are *Q. tomentella* and *H. arbutifolia*, followed by *B. pilularis* and *Q. pacifica*. The positive effect of nurse plants may be due to a combination of fog drip and the leaf litter that accumulates below nurse plants (Kindsvater 2006, Fischer et al. 2009, Evola and Sandquist 2010, Schumann et al. 2014). This combination creates not only a favorable germination substrate, but also enough soil moisture and nutrients for growth and survival over the long term. The presence of a nurse plant also indicates that suitable soils are already present at that location, an important consideration given the elevated levels of historic erosion on the highland ridges of SRI.

Although the larger and taller canopies of *Q. tomentella* or *H. arbutifolia* are more effective at fog capture, we suggest that *B. pilularis* is an important species to manage for ecosystem restoration. *Baccharis pilularis* is a wind-dispersed species that is well adapted to growing in disturbed environments, and it can also contribute moisture from fog drip. *Baccharis pilularis* was observed growing on the outskirts of the island oak groves, and is a relatively easy species to establish and maintain over the long term. Establishing such disturbance-adapted shrubs as nurse species may be important in areas impacted by erosion to build the soil resources necessary for the establishment of *Q. tomentella* and other large woody species such as *H. arbutifolia* and *Q. pacifica*.

Adenostoma fasciculatum and *Arctostaphylos confertifolia* are not effective as nurse species. This may be due to the low mat-growing growth form of *A. fasciculatum* that does not promote abundant fog drip and the unfavorable rocky convex slopes that both *A. fasciculatum* and

A. confertifolia more commonly grow on. However, these species may contribute to other aspects of ecosystem restoration.

This study indicates that *Q. tomentella* regeneration and grove expansion is occurring at Black Mountain. Kindsvater (2006) developed a spatial model projecting potential core habitat for *Q. tomentella* from her mapped distribution of occupancy and seedling/sapling distributions. She estimated that 7% to 8% of SRI had characteristics of elevation, slope, and aspect that matched sites where *Q. tomentella* was growing and recruiting. In 2004, recruitment was occurring in about 1% of those projected areas. Our results generally match the pattern of core habitat predicted by the model in the Black Mountain area.

More research is needed to understand *Q. tomentella* cloning, dispersal, and seedling establishment. The pattern of outlier seedling and sapling distribution indicates that abundant tree regeneration occurs beyond the areas proximate to adult trees where root suckers typically appear. However, it is not known what proportion of the outlier trees have resulted from sexual versus asexual reproduction. We observed few instances of bird and mammal dispersion, but it is possible that caches are present but not observed in the field. Future research will focus on field observations of bird and mammal behavior to better elucidate patterns of acorn dispersal. Differentiating between gravity dispersion and cloning is difficult without digging up roots. Future research will also focus on understanding the relationship between *Q. tomentella* regeneration and terrain (slope steepness, curvature, aspect, elevation), fog capture, and leaf litter accumulation. Identifying the optimal landforms for island oak regeneration can increase restoration effectiveness. Increasing

the study area to include other parts of SRI and other islands would also increase our understanding of *Q. tomentella* regeneration.

This study provides a baseline of the *Q. tomentella* distribution and regeneration on Black Mountain that can be monitored into the future. Increased understanding of tree distribution, dispersal, and regeneration of this species is vital to developing effective ecosystem restoration management and can guide the allocation and prioritization of National Park Service restoration efforts.

ACKNOWLEDGMENTS

We thank Keith Westcott and The Havasi Wilderness Foundation for funding this research and the CSUCI Santa Rosa Island Research Station for logistical and technical support. Special thanks go to Dr. Don Rodriguez, Dr. Mario Pesendorfer, Dr. Scott Sillett, Ryan Summers, Tess Silvestri, and the ESRM 428 Intermediate GIS and ESRM 499 Capstone classes. Without these funders, advisors, and students, this project could not have happened. Any use of trade, product, or firm names in this publication is for descriptive purposes only and does not imply endorsement by the U.S. Government.

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Received 1 March 2017

Revised 16 January 2018

Accepted 14 March 2018

Published online 17 December 2018