Vegetation phenology and habitat discrimination: Impacts for *E. multilocularis* transmission host modelling

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ABSTRACT

Echinococcus multilocularis (Em), a parasitic tapeworm, is responsible for a significant burden of human disease across continental Asia. Here, we use a time-series of MODIS 16-day 250 m Enhanced Vegetation Index (EVI) satellite data to quantify the seasonal vegetation dynamics across a study area in Serxu County, Sichuan Province, China, in relation to the presence of the Em intermediate host *Ochotona curzoniae* (plateau pika) and *Ochotona cansus* (Gansu pika) (here merged to *Ochotona* spp.). A series of derived phenological metrics are analysed using the random forests statistical method to determine the relative importance of seasonal vegetation characteristics. Results indicate negative relationships between *Ochotona* spp. presence and EVI showing a preference for low-biomass habitats. However, EVI values during green-up and senescence periods are also shown to be important, potentially resulting from improved detectability of low-biomass grassland habitats at these times. Improved detection of *Ochotona* spp. preferred habitats via time-series EVI imagery offers better understanding of the distributions of this Em host, and the potential for monitoring the changes in *Ochotona* spp. optimal habitat distributions resulting from landscape change. This could aid the identification of villages at increased risk of infection, enabling preventive strategies to be adopted.

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1. Introduction

Human Alveolar Echinococcosis (HAE) caused by the parasitic tapeworm *Echinococcus multilocularis* (Em) is an emerging pathogen for which recent prevalence and range expansion has been documented (Combes et al., 2012; Eckert, 1996; Eckert, Gemmell, Meslin, & Pawlowski, 2001). Present within Europe, North America, Central Asia, China, Japan, and the former USSR, it is a highly pathogenic zoonosis (Ammann & Eckert, 1996), with over 94% mortality in untreated patients ten years after diagnosis (Wang et al., 2010). The spatial distribution of Em is highly variable, with significant regional and local differences in parasite prevalence resulting in patchy distributions of endemicity (Eckert et al., 2001; Giraudoux et al., 2006; Giraudoux, Raoul, Afonso, Ziadinov, Yan, et al., 2013) within which transmission hotspots of much larger prevalence may occur (Danson, Craig, Man, Shi, & Giraudoux, 2004; Said-Ali et al., 2013). Examples include Gansu

and Sichuan Provinces, China, where prevalence rates of >10% have been observed locally (Craig et al., 1992; Li et al., 2010).

1.1. Transmission cycle

The Em transmission cycle is based on the predator–prey relationships between definitive hosts, such as fox, and small mammal intermediate hosts (Eckert et al., 2001; Rausch, 1995). Adult tapeworms within a definitive host produce eggs at regular intervals which are shed in host faeces, contaminating the environment (Raoul et al., 2001). The parasite lifecycle then undergoes a 'free-egg' stage, where viable eggs are available in the environment, before intermediate hosts are infected through oral ingestion of eggs when feeding (Eckert, 1996). The transmission cycle is completed when definitive hosts are infected through predation of infected intermediate hosts (Fig. 1). Domestic dogs are also susceptible to infection, and due to their close contact with people are considered a significant infection risk to human populations (Moss et al., 2013; Rausch, 1995). Human infection occurs due to accidental ingestion of Em eggs from direct contact or via food contaminated by canid definitive host faeces (Giraudoux, Raoul, Pleydell, Li, Han, et al. 2013).

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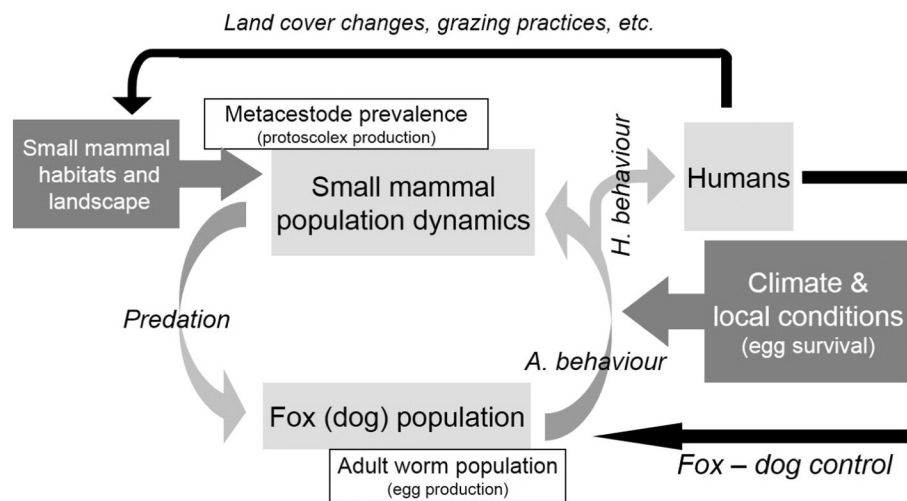 *E-mail address:* marstonc@edgehill.ac.uk (C.G. Marston).

Fig. 1. *E. multilocularis* transmission cycle.
Adapted from Giraudoux et al. (2003).

Domestic dogs have been identified as a major transmission source to humans in Gansu Province, and the eastern Tibetan plateau, China, respectively (Craig et al., 2000; Wang et al., 2010), with Em infection rates in dogs of up to 33% recorded in western Sichuan Province, China (Budke, Campos-Ponce, Wang, & Torgerson, 2005).

Reinfection studies in this area suggest that domestic dog populations are quickly re-infected by Em, and may contribute to an active peri-domestic transmission cycle (Giraudoux, Raoul, Afonso, et al., 2013; Moss et al., 2013). The Em worm burden in dogs has also been shown to have a positive statistically significant relationship with maximum burrow densities of the plateau pika (*Ochotona curzoniae*), an important Em intermediate host (Giraudoux et al., 2006), in the surrounding landscape in Shiqu County, China (Wang et al., 2010). This suggests that the rapid Em re-infection rates in domestic dogs, as shown by Moss et al. (2013), can be linked to surrounding high densities of *Ochotona* spp.

1.2. Small mammal–landscape linkages

Small mammal distributions are often influenced by the locations of key favourable habitats and land cover types (Raoul et al., 2008). Landscape change has, in turn, been demonstrated to modify small mammal distributions in China as a result of deforestation (Giraudoux et al., 1998; 2003), afforestation (Raoul et al., 2008), and farming and fencing practices (Raoul et al., 2006; Wang et al., 2004). Landscape change impacting these favourable habitat distributions can also affect small mammal population dynamics (Lidicker, 2000), resulting in pathogen transmission varying through space and time due to landscape modification.

Overgrazing, resulting in pasture degradation, is linked to increased densities of *Ochotona* spp., *Microtus* (vole) spp., *Cricetulus kamensis* (Tibetan dwarf hamster), and *Eospalax fontanierii* (mole rat) (Hou, 2001; Raoul et al., 2006; Wang et al., 2006) on the eastern Tibetan plateau, China, where HAE is endemic (Li et al., 2010; Wang et al., 2004). Wang et al. (2010) also reported grass height as negatively related to burrow abundance of *O. curzoniae*, indicating that overgrazing increased the abundance of this species. With high densities of *O. curzoniae* significantly associated with infection of domestic dogs (Wang et al., 2010), foxes, and humans (Craig et al., 2000), pastureland degradation resulting from overgrazing could prove a significant driver of increased Em infection in humans in this region. On the Eastern Tibetan Plateau *O. curzoniae* shares its geographical distribution with several other small mammal species found to be infected with *E. multilocularis* including *Microtus leucurus* (Blyth's vole), *Microtus limnophilus*

(lacustrine vole), *Microtus fuscus* (smokey vole), *Microtus irene* (Chinese scrub vole), and *C. kamensis* (Tibetan dwarf hamster). *O. curzoniae* can, however, be considered a flagship species for transmission in this area due to its easy detectability (Giraudoux, Raoul, Afonso, et al., 2013) and established links with Em infection in dogs (Wang et al., 2010). The species is diurnal and has a widely spread and high population, contrasting with more localised populations of Microtus spp. in Shiqu county.

1.3. Remote sensing for landscape-disease studies

Remote sensing has emerged as an important tool in the surveillance and forecasting of zoonotic infectious diseases (Wayant, Maldonado, Rojas de Arias, Cousiño, & Goodin, 2010), with satellite-derived landscape information related to small mammal-borne diseases such as leptospirosis (Herbreteau et al., 2006), junin virus (Porcasi et al., 2005), sin-nombre virus (Boone et al., 2000), and hantavirus (Glass et al., 2000; Goodin et al., 2006). Studies investigating the relationship between Em and landscape using remote sensing techniques in southern Gansu Province, China, have also previously identified strong links between landscape composition and HAE prevalence (Danson et al., 2004, Giraudoux, Raoul, Pleydell, et al., 2013b). These studies suggested that grassland and tree/shrub habitats capable of sustaining cyclically high populations of susceptible intermediate hosts were key spatial determinants of Em transmission (Danson et al., 2003), and indicated that landscape composition could provide a useful predictor of Em and HAE (Giraudoux et al., 2003; Giraudoux, Raoul, Pleydell, et al., 2013; Pleydell et al., 2008).

Marston et al. (2014), used thematic land cover maps generated from single-date Landsat Enhanced Thematic Mapper imagery, to show that low biomass degraded grassland has a major influence on *Ochotona* spp. presence in the Serxu region of the Tibetan Plateau, China, further illustrating the influence of potentially overgrazed areas on Em host distributions. However, limitations exist when using thematic land cover maps for landscape assessment, including the loss of sub-class landscape variability and difficulties in validating classifications generated from historical data. An alternative approach uses a continuous measure to quantify landscape characteristics such as vegetation indices. Vegetation Indices (VI) have shown consistent correlation with vegetation productivity (Reed et al., 1994), biomass, and dynamics in various ecosystems worldwide (Pettorelli et al., 2005), and have demonstrated good sensitivity for assessing spatio-temporal variations in vegetation amount and condition (De Oliveira, de Oliveira, de Carvalho, Martinhago, & de Freitas, 2009). Vegetation

indices have been used to monitor land and habitat degradation (Holm, Cridland, & Roderick, 2003), vegetation quality for herbivores (Griffith et al., 2002), and subsequent prediction of animal responses (Pettorelli et al., 2005). They have also been linked with species distributions (Osborne, Alonso, & Bryant, 2001), biodiversity levels (Hurlbert & Haskell, 2003; Nagendra, 2001), and the performance and movement patterns of animal populations (Griffith et al., 2002; Pettorelli et al., 2005).

The Enhanced Vegetation Index (EVI) dataset from the Moderate-Resolution Imaging Spectroradiometer (MODIS) sensor enables analysis of spatio-temporal vegetation patterns, while being less susceptible to the limitations of some VI, such as atmospheric aerosols influence and invariance to vegetation condition due to saturation of the chlorophyll signal in densely vegetated canopies (Cao, Cova, Dennison, & Dearing, 2011; Pettorelli et al., 2005). EVI is formulated as:

$$EVI = G * ((N-R)/(N + C_1R - C_2B + L))$$

where N (near-infrared), R (red), and B (blue) are atmospherically-corrected (or partially atmospherically-corrected) surface reflectances, G is a gain factor, C_1, and C_2 are coefficients to correct for atmospheric condition, and L is a soil-adjustment factor. For the standard MODIS EVI product, $L = 1$, $C_1 = 6$, $C_2 = 7.5$ and $G = 2.5$ (Jiang, Huete, Didan, & Miura, 2008).

1.4. Time-series vegetation indices

Seasonal vegetation phenology is well defined (Zhang et al., 2003), with initial leaf emergence typically followed by rapid green-up prior to a stable period of maximum leaf area before senescence, leading to a low leaf area period. Vegetation in different localities exhibits different and distinctive patterns in this phenological profile (Yu, Zhuang, Chen, & Hou, 2004), which cannot be captured by single-date satellite imagery. However, using a dense time-series of VI data relating to vegetation dynamics offers further insights for spatio-temporal vegetation modelling in relation to animal distributions and ecological phenomena (Pettorelli et al., 2005). Previous examples include relating NDVI to avian species richness (Bailey et al., 2004), Caribou calving ground selection (Griffith et al., 2002), and tick (Acari: Ixodidae) distribution in Spain (Estrada-Pena, Quilez, & Sanchez Acedo, 2004). In an epidemiological context multi-temporal satellite VI datasets have been used to relate disease distribution and dynamics to environmental conditions for Rift Valley Fever (Linthicum et al., 1999), malaria (Thomson et al., 1999), and hantavirus (Cao et al., 2011; Glass, Shields, Cai, Yates, & Parmenter, 2007).

1.5. Aims

The aim of this study is to investigate factors relating to the transmission dynamics of *E. multilocularis*, by using MODIS time-series 250 m resolution VI data to quantify regional-scale vegetation phenology metrics across an area of the Tibetan Plateau. We investigate the key question of whether the distributions of colonies of the transmission host *O. curzoniae* and *Ochotona cansus* (*Ochotona* spp., see below), as identified by field survey, exhibit specific trends connected to seasonal landscape phenological patterns. We look to identify and characterise the key vegetation phenological metrics, and their relative importance, in influencing the spatial distribution of *Ochotona* spp.

2. Materials and methods

2.1. Study area

The study area is located close to the town of Tuanji, Shiqu County, Sichuan Province, China (Latitude 33.04°N Longitude 97.97°E) (Fig. 2). Located at altitudes between 4000 and 4300 m above sea level on the

Tibetan plateau, the site is dominated by semi-natural grassland, with variation in herb and shrub vegetation layers producing a variety of land cover types. Extensive areas of degraded grassland are present as a result of heavy grazing by Yak, with at least three townships in Shiqu county shown to be local foci for HAE, indicating that a transmission cycle is, or has previously been active here (Wang et al., 2001).

Field surveys conducted in July 2001 comprised fifteen transects of varying length (220–4750 m) totalling approximately 35 km, with transect routes selected to sample the full range of land cover types present. Indicators of small mammal activity were recorded for each ten metre survey interval along a transect line, with a total of 3481 ten metre survey intervals recorded. Visual sightings of small mammals and species-specific indicators including foraging corridors, ground holes, and small mammal faeces, identifiable to species or genus level (Raoul et al., 2006; Wang et al., 2010), were used as evidence of small mammal presence using methods established by Giraudoux et al. (1998). Although densities of *Ochotona* spp. may vary seasonally with summer increases and winter decreases in density, colonies are relatively geographically stable through time, and therefore presence or absence of *Ochotona* spp. rather than population densities was determined. Transect routes were mapped with hand-held Global Positioning System (GPS) receivers with an accuracy of approximately 15 m.

Raoul et al. (2006) determined the small mammal community in this area to be comprised of *M. irene* (Chinese scrub vole), *M. limnophilus* (lacustrine vole), *M. leucurus* (Blyth's vole), *C. kamensis* (Kam dwarf hamster), and two Ochotonid species, *O. curzoniae* (plateau pika), and *O. cansus* (Gansu pika), the latter being recorded sporadically compared to the former. Given the extensive *Ochotona* spp. colonies in the study area, and the established links between Em infection in dogs and *Ochotona* spp. (Wang et al., 2010), this investigation focused on the *Ochotona* species. Due to similarities between the two species resulting in identification difficulties, these were merged to form a generic *Ochotona* spp. group.

2.2. MODIS time series imaging processing

MODIS EVI 16-day composite 250 m resolution (MOD13Q1) imagery providing complete temporal coverage from 2001 to 2013 (299 images in total) was acquired and reprojected into UTM WGS84 Zone 47 N projection. A de-noising procedure using inverse Fourier Transform (Wayant et al., 2010) was applied to the time-series EVI dataset using IDRISI 17.02 to minimise potential sources of data error. The de-noised EVI values were extracted for the complete time-series for each transect interval. Mean EVI values were calculated for twenty three sixteen-day MODIS 16-day compositing periods (CP) across the whole time series (CP dates shown in Table 1) for every transect interval. To quantify the vegetation seasonal cycle, a series of phenological metrics were extracted (Reed et al., 1994) (Table 2) using the Timesat software package (Jönsson & Eklundh, 2002, 2004).

To identify which compositing period and phenological metrics are of greatest importance in relation to *Ochotona* spp. presence, random forest analysis was performed (environmental variables = 37 (comprised of the 23 compositing periods (Table 1) and the 14 phenological metrics (Table 2)), number of trees = 5000, variables tried at each split = 12). Random forests (RF) is an ensemble learning technique developed by Breiman (2001) based on a combination of a large set of classification and regression trees. This method is well-suited to handling large datasets with correlated predictor variables which can be non-parametric, comprise a variety of data types, and where no assumption of independence concerning the data being analysed is made (Perdiguero-Alonso, Montero, Kostadinova, Raga, & Barrett, 2008). In addition, the technique is robust to over-fitting, noise and outliers (Breiman, 2001; Marston et al., 2014). Two-thirds of the data is used to train the RF with the remaining third, the 'out of bag' (OOB) samples, retained for RF prediction error testing, removing the need for cross-validation via a separate test dataset (Perdiguero-Alonso
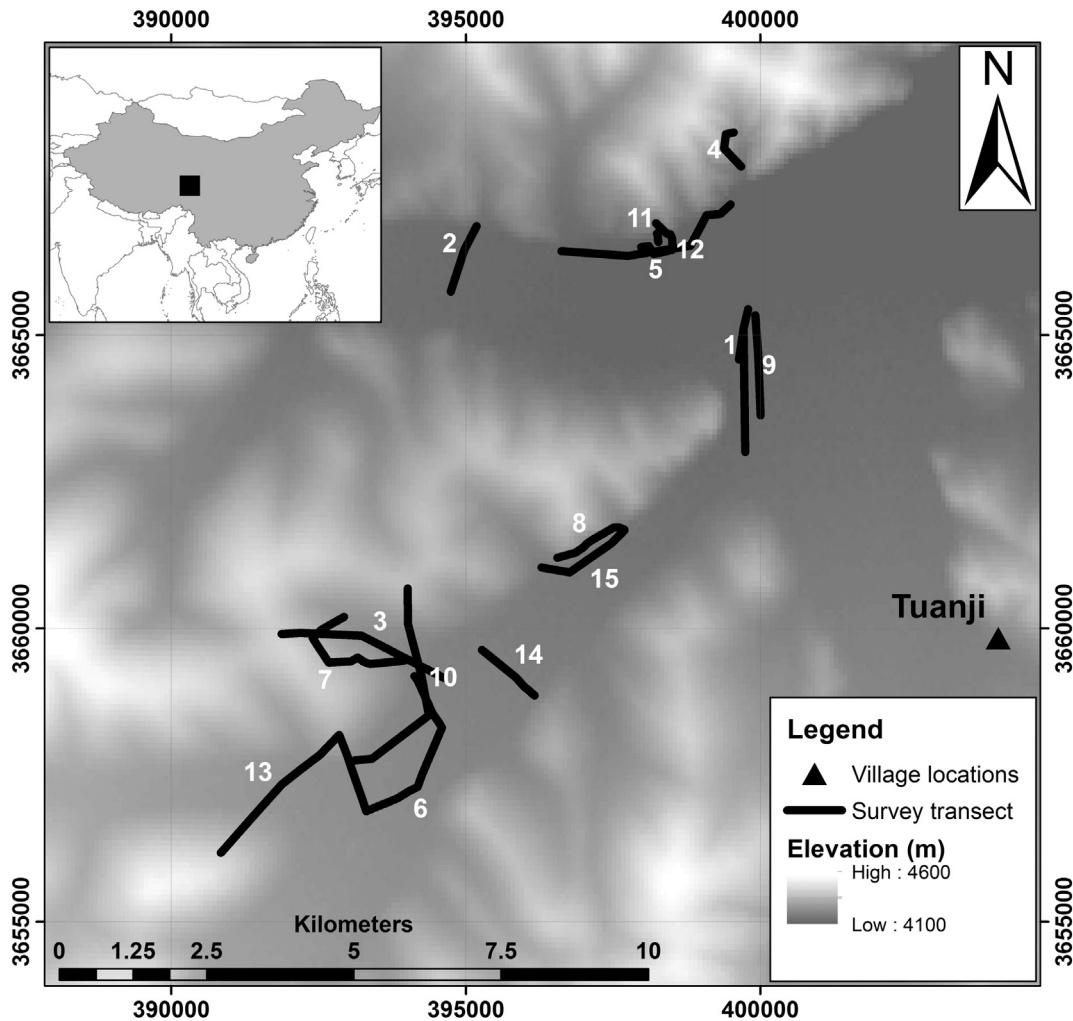
Fig. 2. Study site location with numbered survey transects, SRTM DEM (USGS, 2004) site elevation and UTM WGS84 zone 47 N grid displayed.

et al., 2008). Variable importance rankings are generated by comparing increases in OOB error when a variable is randomly permuted while all others remain unchanged (Abdel-Rahman, Ahmed, & Ismail, 2013),

Table 1
MODIS 16-day compositing period imagery acquisition dates.

Compositing period (CP)	Julian day start and finish
1	1–16
2	17–32
3	33–48
4	49–64
5	65–80
6	81–96
7	97–112
8	113–128
9	129–144
10	145–160
11	161–176
12	177–192
13	193–208
14	209–224
15	225–240
16	241–256
17	257–272
18	273–288
19	289–304
20	305–320
21	321–336
22	337–352
23	353–365 +

enabling importance ranking of the variables in relation to *Ochotona* spp. presence (Fig. 3). Random forest analysis was performed in the R statistical environment using the randomForest package (Liaw & Wiener, 2002). In addition, to measure the strength and direction of the association between *Ochotona* spp. presence or absence, and the phenological metrics and CP values, point-biserial correlations were calculated. Point-biserial correlation is a special case of Pearson's product–moment correlation for assessing the correlations between one dichotomous (such as presence or absence) and one continuous variable.

3. Results

The RF variable importance plot (Fig. 3) displays the relative importance of each phenological metric and compositing period (CP) mean EVI variable in relation to *Ochotona* spp. presence. This shows the EVI values for CP8 (Julian day 113 to 128) and CP7 (Julian day 97 to 112) to be highest ranked, suggesting EVI values during spring are of greatest importance in relation to *Ochotona* spp. presence. Of the phenological metrics, RD (3rd ranked), BV (4th), Minimum EVI (5th), EOS (6th), and PMS (8th) were among the more important variables. The high ranking of BV suggests that the minimum levels of vegetation throughout the year is important, however vegetation condition at certain periods within the phenological cycle (CP8 and CP7), and the senescence period (as shown by RD) have the greatest influence on *Ochotona* spp. presence.
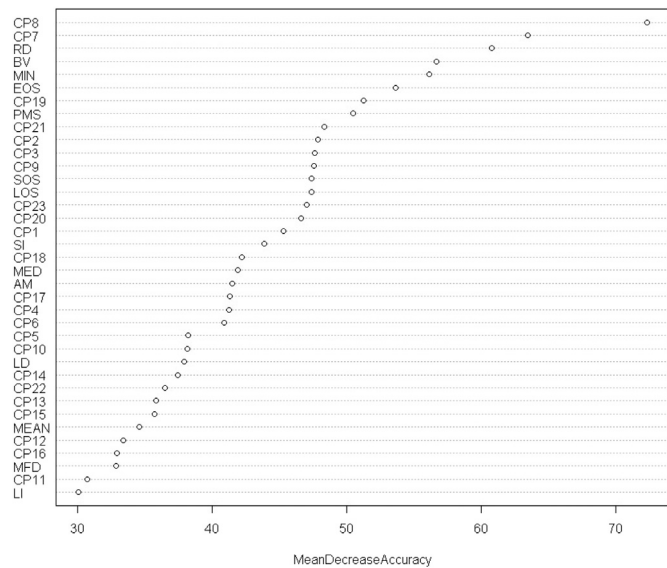
Point-biserial correlation values between *Ochotona* spp. presence and the CP and phenological variables were calculated (Table 3),

Table 2
Phenological metrics calculated.
Adapted from Eklundh and Jönsson (2009) and Pettorelli et al. (2005).

Phenological metric	Acronym	Definition
Annual minimum VI	MIN	Minimum VI value over a year.
Annual mean VI	MEAN	Mean VI value over a year.
Median VI	MED	Median VI value over a year.
Annual VI amplitude	AM	Difference between maximum and minimum VI values; maximum increase in canopy photosynthetic activity above the baseline.
Start of season	SOS	Day of year identified as having a consistent upward trend in time series VI; start of the green-up period.
End of season	EOS	Day of year identified at the end of a consistent downward trend in time series VI; end of the senescence.
Length of season	LOS	Number of days between SOS and EOS.
Large seasonal integral	LI	Integral of the function describing the season from the season start to season end; canopy photosynthetic activity across the entire growing season.
Small seasonal integral	SI	Integral of the differences between the function describing the season and the base level from season start to season end.
Base value	BV	Given as the average of the left and right minimum values.
Position of middle of season	PMS	Time for the middle of the season. Computed as the mean value of the times for which, respectively, the left edge has increased to the 80% level and the right edge has decreased to the 80% level.
Maximum of fitted data	MFD	Largest data value for the fitted function during the season; maximum level of photosynthetic activity.
Left derivative	LD	Rate of increase at the beginning of the season. Calculated as the ratio of the difference between the 20% and 80% levels and the corresponding time difference.
Right derivative	RD	Rate of decrease at the end of the season. Calculated as the absolute value of the ratio of the difference between the right 20% and 80% levels and the corresponding time difference.

Table 3
Point-biserial correlation values between *Ochotona* spp. presence and CP and phenological variables. Exact p-values are reported, with a p-value of <0.05 considered significant.

Variable	Pearson's correlation	p-Value
CP1	−0.104	<0.0001
CP2	−0.040	0.0180
CP3	−0.019	0.2562
CP4	−0.044	0.0095
CP5	−0.128	<0.0001
CP6	−0.289	<0.0001
CP7	−0.433	<0.0001
CP8	−0.428	<0.0001
CP9	−0.370	<0.0001
CP10	−0.316	<0.0001
CP11	−0.272	<0.0001
CP12	−0.239	<0.0001
CP13	−0.218	<0.0001
CP14	−0.207	<0.0001
CP15	−0.210	<0.0001
CP16	−0.229	<0.0001
CP17	−0.266	<0.0001
CP18	−0.316	<0.0001
CP19	−0.355	<0.0001
CP20	−0.359	<0.0001
CP21	−0.331	<0.0001
CP22	−0.273	<0.0001
CP23	−0.184	<0.0001
AM	−0.104	0.0006
BV	−0.407	<0.0001
EOS	−0.031	0.0655
LD	−0.173	<0.0001
LI	−0.266	<0.0001
MFD	−0.214	<0.0001
PMS	−0.041	0.0164
RD	−0.062	0.0003
SI	−0.058	0.0006
SOS	−0.277	<0.0001
LOS	0.262	<0.0001
Min	−0.376	<0.0001
Mean	−0.302	<0.0001
Median	−0.282	<0.0001

illustrating the strength (Pearson's correlation) and direction (positive or negative) of the associations present. All relationships observed were negative with the exception of LOS. When the correlations between *Ochotona* spp. presence and CP variables were plotted (Fig. 4),

two peaks of negative correlation are observed, with the strongest negative correlations observed at CP7 (−0.433) and CP8 (−0.428), with weaker correlations observed for CP9 to CP18. The second peak is observed at CP19 (−0.355) and CP20 (−0.359), before correlation strengths begin to decline. The weakest relationships observed are at the beginning of the year for CP2 (−0.04). Correlations between *Ochotona* spp. presence and phenological metrics varied from the strongest relationships of −0.407 for BV, −0.376 for minimum VI and −0.302 for mean VI to the weakest of −0.031 for EOS. The only metric
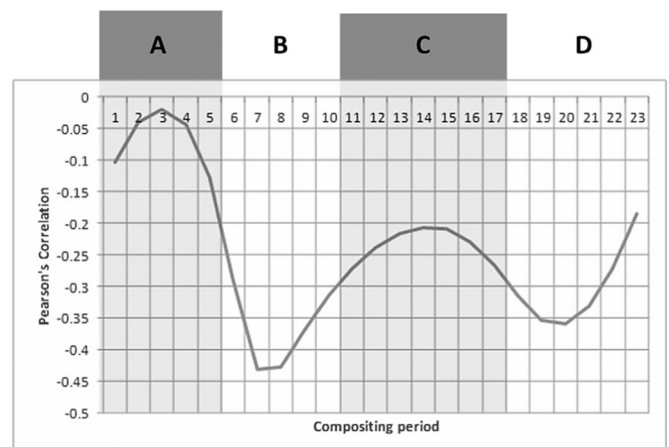

Fig. 3. Random forest variable importance plot. Variables are ranked in terms of importance on the Y axis (with variables of highest importance at the top), with mean decrease in accuracy should that variable be removed from the random forest on the X axis.

Fig. 4. Correlations between *Ochotona* spp. presence and CP mean EVI.

which showed a positive correlation with *Ochotona* spp. presence was again the length of season variable (LOS; 0.262).

4. Discussion

This study examined the relationships between time-series EVI data and *Ochotona* spp. presence to identify the key vegetation phenological metrics influencing *Ochotona* spp. presence in the context of the *E. multilocularis* transmission cycle. Previous studies indicated that *Ochotona* spp. colonies were more commonly present in low cover vegetation areas (Marston et al., 2014; Raoul et al., 2006). This study supports this with consistent negative correlations observed between *Ochotona* spp. presence and EVI and phenological metric variables. The relationship strength between *Ochotona* spp. presence and BV (−0.407) (quantifying minimal levels of biomass throughout the phenological cycle), shows presence to be more likely where the annual minimal level of vegetation is lowest. However, the higher correlations between EVI values and *Ochotona* spp. presence displayed in spring (CP7–9) and autumn (CP18–21), in combination with CP8 and CP9 ranked as the most important RF variables, suggests that biomass levels at certain periods of year were also key. Similar seasonal patterns are observed by Cao et al. (2011) while investigating the small-mammal borne Sin Nombre virus, who found that correlations between VI values and deer mouse (a primary host) density as well as the number of infected deer mice typically peaked in May or June. This suggests that the importance of key phenological stages when investigating landscape and small mammal linkages is applicable beyond our study area and *Ochotona* spp.

However, the peaks in point-biserial correlation values in spring and autumn (Fig. 4) could be a function of the ability of MODIS EVI data to discriminate between areas of low biomass degraded grassland and other habitats at certain times of year. Fig. 4 identifies four phases of varying point-biserial correlation strength. Period A corresponds to winter when vegetation biomass is very low with frequent snow cover, resulting in no clear distinction between degraded grassland and other habitats within the EVI dataset. During period B intensive vegetation growth occurs resulting in clear contrasts between low-biomass degraded and other non-degraded habitats. During period C vegetation has also grown in the degraded areas (with some delay as low biomass areas are likely to be slower to produce a measureable increase) which, coupled with reduced grazing due to the departure of yak to their summer pastures, results in decreased contrasts between degraded and non-degraded areas. Period D corresponds to vegetation growth ending due to the onset of autumn/winter and increased grazing as yak return from their summer pastures. This leads to increased discrimination between degraded and non-degraded habitats due to the reduction in biomass occurring more quickly at the degraded sites due to the lower existing levels of standing biomass. This is consistent with the high importance ranking of RD (right derivative), which corresponds to the rate of decrease in VI values at the end of the growth season. Consequently, the low-biomass degraded grassland habitats important in influencing *Ochotona* spp. presence may be better discriminated from other habitats at certain phenological phases. This could aid optimal targeting of future surveys for more focused landscape modelling in relation to disease reservoir species distribution.

The heavy grazing by yak and resultant grassland degradation within the study area is of particular concern, as previous studies have shown changes in grazing practices and land cover can increase the likelihood of the small mammal outbreaks suggested to play a significant role in Em transmission (Li, 1995; Wang et al., 2004). If overgrazing continues to increase grassland degradation, expansions in *Ochotona* spp. distributions resulting in closer proximity to villages are likely to result in greater infection risk to domestic dogs. Although the role of Microtine species in disease transmission in this area cannot be discounted, the extension of *Ochotona* spp. colonies closer to villages containing dogs increases potential human exposure to parasite eggs, and infection risk to local communities.

Here, multi-temporal landscape characterisation using VIs have been applied within an epidemiological context, with results showing that the MODIS 16-day composite VI data product has sufficient sensitivity to track the seasonal vegetation phenology at this study site. Although the 250 m resolution of this imagery means multiple land cover types could potentially be contained within a single pixel, the relatively homogenous grassland dominated areas within this study site suggest that the use of MODIS time-series VI datasets is appropriate for capturing the landscape and vegetation dynamics at an ecologically meaningful scale. By using satellite VI data as a surrogate measure of biophysical characteristics of the landscape and capturing the dynamic vegetation and phenological characteristics driving the biological systems of that site (as previously performed by Lunetta, Knight, Ediriwickrema, Lyon, & Worthy, 2006), a better description of the fundamental variability of the landscape can be achieved, and the links between seasonal landscape dynamic and small mammal parasite transmission reservoirs better understood. The potential influence of small mammal population cycles must also be acknowledged (evidence has been provided that *O. curzoniae* populations on the eastern Tibetan plateau can be cyclic, with cycle duration >6–7 years (Giraudoux et al., 2006)), meaning that *Ochotona* spp. habitats defined by the signal captured by MODIS EVI 16-day may correspond to periods when *Ochotona* spp. are locally scarce during the low density phase of a cycle (Giraudoux et al., 2007). However, while *Ochotona* spp. densities may vary due to multi-annual population cycles, their colonies are geographically very stable over several years (Giraudoux, personal communication, May 1, 2015), meaning that the methodological approach employed at this site is both appropriate and highly informative in this context.

The use of random forests to identify key phenological variables linked to *Ochotona* spp. and the potential to apply these techniques over broad geographical areas could contribute significantly to understanding the broader Em transmission pathways between *Ochotona* spp. small mammal intermediate hosts, both sylvatic (fox) and domestic (dog) definitive hosts, and susceptible human populations. By identifying likely areas of *Ochotona* spp. presence based on seasonal landscape dynamics and vegetation levels at certain phases of the phenological cycle, areas where domestic dogs are at risk of continual re-infection by Em may be better determined. This could be particularly important given the relationships established previously by Wang et al. (2010) correlating density of *Ochotona* spp. burrows with domestic dog infection rates, and could aid the design of pre-emptive disease control measures including targeted antihelminthic treatment of dogs to reduce the Em infection risk to local human populations. Similar analysis methods could also be suitable for extension to other small mammal-borne diseases around the globe (Cao et al., 2011), for example for leptospirosis, Argentine haemorrhagic fever, sin nombre virus and hantavirus.

5. Conclusion

The use of high-temporal-resolution MODIS imagery in epidemiological studies has been limited to date (Cao et al., 2011), however this study demonstrates the potential for using MODIS time-series satellite imagery in identifying the dynamic landscape variables important in influencing *Ochotona* spp. presence. Given the cost-free availability of MODIS data and its global coverage, these methods can potentially be extended to model the landscape dynamic – small mammal relationships for other small mammal-borne diseases elsewhere in the world. This could be used to predict the ecological effects of environmental change on ecosystem functioning and animal population distributions (Pettorelli et al., 2005), and offer insights as to how these changes influence small mammal disease transmission hosts, and human populations at risk of infection. By identifying the key phenological variables in

relation to *Ochotona* spp. given its importance as a key intermediate host for *E. multilocularis*, there is potential to better predict Em transmission foci locations and HAE risk. In combination with the improved targeting of remote sensing data collection enabling improved discrimination of habitats of interest and modelling of disease host distributions, this could better inform the development of disease control strategies to reduce transmission to humans in this region. While these results are promising, further research with a longer time series of satellite imagery and small mammal sampling data would enable the impacts of landscape change on Em host populations, and therefore disease transmission risk, to be determined.

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