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Crossing the western Altiplano: The ecological context of Tiwanaku migrations

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ABSTRACT

Mobility and migration are critical processes that influence cultural and socio-economic development, and have lasting effects on demographic and ecological arrangements. However, these are ephemeral behaviors which are difficult to reconstruct archaeologically. Here, we employ geospatial approaches to reconstruct mobility corridors likely used by Tiwanaku migrants during the Andean Middle Horizon, ca. AD 500–1000. Prehispanic mobility relied on caravans of Andean camelids. We reconstruct probable mobility corridors while comparing cost- and permeability-based modeling approaches. We further use remote sensing to examine how modern ecological dynamics relate to modeled mobility corridors. Imagery from the Landsat family of multispectral satellites is used to document the response of green vegetation to seasonal and interannual moisture variability. We find that there is a statistically significant increase in the amount of perennially-green vegetation land cover along the corridor linking Tiwanaku with its principal colonial enclaves on the Pacific coast. Such perennially-green vegetation provides a critical resource for prehispanic caravans. The data indicate a relationship between high volumes of migration and enhanced vegetation. We explore whether Tiwanaku migration routes were established in part on the basis of this resource, or if modern land cover reflects an anthropogenic legacy.

1. Introduction

Migration is a key factor in the development of premodern states, which has profound long-term effects on demographic, socio-political and settlement reorganizations; the diffusion of technological and economic strategies; and ecological transformations. During the Andean Middle Horizon period (ca. AD 500–1000), two prehispanic states—Wari and Tiwanaku—expanded out of highland centers to developed demic colonies and indirect political-ecological networks spanning the central Andes. By approximately AD 600, Tiwanaku had established colonial communities and connections to economic resources throughout the Lake Titicaca basin, adjacent Pacific lowland valleys, and on the edges of the Amazonian region. Prior archaeological studies have examined the effects of these migrations on Tiwanaku populations and economics in both its urban center as well as colonies; here, we examine ecological dynamics of the highland Altiplano that facilitated Tiwanaku mobility networks and discuss the implications of prehispanic mobility on the long-term ecological organization of the Altiplano.

Specifically, our analysis focuses on the association between modeled migration corridors and the distribution of vegetation communities. Prehispanic Andean migrations were enabled by caravans that used camelids both as pack animals and as commodities themselves. Caravan logistics are constrained by ecological conditions. In particular, vegetation cover in high elevations and arid – semi-arid portions of the Andes —the availability of quality pasturage—represents a significant limiting factor on the ability to manage large numbers of camelids, both as resident herds and transient caravans (Kuznar, 1991a; Nielsen, 2001).

Here, we use geospatial approaches to model probable mobility corridors used to articulate urban Tiwanaku with important areas of the western Pacific Valleys between Arequipa and Tacna, Peru. We subsequently use remote sensing to evaluate the distribution and response of vegetation resources within this region, in particularly focusing on the availability and permanence of perennially-green vegetation that could have provided high quality pasture to caravan animals throughout all periods of the year.

Our analysis shows a statistically significant relationship between Tiwanaku migration corridors (both modeled using geospatial methods and demonstrated archaeologically) and a greater amount of perennially-green vegetation cover. The strongest relationship is found within the corridor linking Tiwanaku with Moquegua, where the

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strongest evidence for direct colonization and bidirectional migration has been found to date (Baitzel and Goldstein, 2016; Goldstein, 2005, 1985; Goldstein and Owen, 2001; Knudson et al., 2014). We propose that this relationship facilitated more intensive traffic between Tiwanaku and its principal colonies on the Pacific coast of South America. Further, we explore the hypothesis that the greater availability of green vegetation may be related to more intensive Tiwanaku activity in this region, which had long lasting ecological effects.

2. Archaeological and environmental setting

Our study region is a portion of the south-central Andes between approximately 15°–18° S latitude and 68° 30' – 72° 30′ W longitude, encompassing the western Lake Titicaca watershed and the interandean and Pacific valleys between Colca and Caplina (Fig. 1). We further subset this overall region of interest (ROI) to focus on a corridor between Desaguadero and Moquegua. Elevations range from 0 to 6200 m above sea level (masl). The Altiplano—a broad, intermontane plateau between 3600 and 4500 masl—represents about 53% of the study region. Modern and prehispanic occupation is densest in the Pacific valleys and around Lake Titicaca; sparsely distributed throughout the rest of the Altiplano, and effectively absent from the intervalley Pacific coastal desert. At elevations below approximately 3600 masl, various agricultural strategies are common. Above these elevations, resident groups rely on agropastoral and specialized pastoral economies (Flores Ochoa, 1979). The availability of vegetation suitable for pasturing camelids is central to reconstructing both past herding and caravanning activities.

2.1. The spread of Tiwanaku in the south central Andes

During the Middle Horizon period, ca. AD 500–1000, the Tiwanaku state developed in the Lake Titicaca basin of Peru and Bolivia, and expanded into adjacent portions of the central Andes (Albarracin-Jordan, 1996; Bennett, 1950; Browman, 1978; Janusek, 2004; Kolata, 1996). Tiwanaku sites are most prevalent along Lake Titicaca's southern shorelines and islands within the lake (Bauer and Stanish, 2001; Janusek and Kolata, 2003; Smith and Janusek, 2014; Stanish, 2009; Stanish et al., 1997).

Tiwanaku's economic, political, and cultural relationships, including the state's direct influence, with peripheral regions outside of the Titicaca Basin are the subject of some discussion. Tiwanaku networks were extensive and incorporated most of the western Pacific Valleys between Majes, Peru and Azapa, Chile. Tiwanaku sites and Tiwanaku-affiliated cultural materials are reported at Uchumayo, Socabaya, and Kasapatac

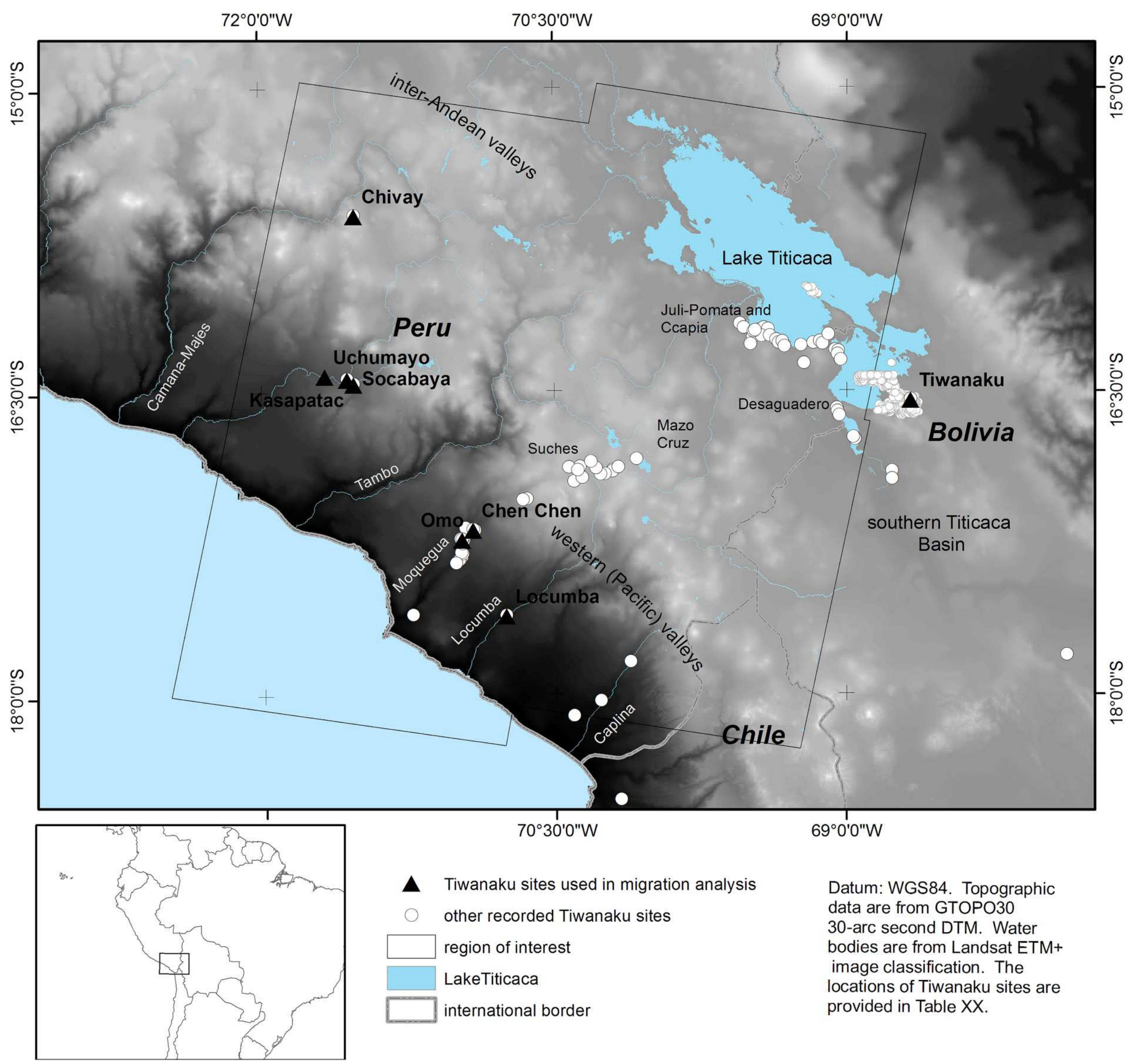

Fig. 1. The study region with the locations of sites and regions mentioned in the text.

in the Arequipa Valley (Cardona Rosas, 2010), Omo and Chen Chen site complexes in Moquegua (Goldstein, 2005, 1985; Goldstein and Owen, 2001), and Locumba, Sama, and Caplina Valleys of southern Peru and the Azapa Valley of northern Chile; and the San Pedro de Atacama region (Baitzel and Rivera Infante, 2019; Berenguer, 2000; Goldstein, 1995; Korpisaari et al., 2014; Mujica et al., 1983; Muñoz Ovalle and Gordillo Begazo, 2016; Owen, 2005; Stovel, 2008; Torres-Rouff et al., 2015; Vela, 1992). Kołomański (2016) recently has reported Tiwanaku materials in 47 graves at the site of La Pampilla 1 in the Tambo Valley; these funerary contexts date late in the Middle Horizon/early LIP. Obsidian from the Chivay source is most prevalent at Tiwanaku itself as well as Tiwanaku-affiliated sites like Omo and Chen Chen (Burger et al., 2000; Glascock and Giesso, 2012; Tripcevich, 2010), indicating that access to this resource was important during Tiwanaku's economic expansion. However, Tiwanaku occupation sites have yet to be reported for Chivay and the Tambo Valley, despite surveys in both regions (Doutriaux, 2004; Kołomański, 2016; Tripcevich and MacKay, 2011; Wernke, 2013).

The distribution of Tiwanaku sites both within the Titicaca Basin and elsewhere suggests that state's expansion focused on strategic nodes and communication networks linking them (Albarracin-Jordan, 1996; Janusek and Kolata, 2003; Smith and Janusek, 2014; Stanish, 2009, 2003; Stanish et al., 1997). Strong bioarchaeological and archaeological evidence, including the greatest density of Tiwanaku-related settlements outside the Titicaca Basin, suggests Tiwanaku established direct demic, economic, and cultural colonies at Omo and Chen Chen (Baitzel and Goldstein, 2016; Blom et al., 1997; Goldstein, 1985; Goldstein and Owen, 2001, 2001; Knudson, 2008).

The evidence for direct colonies in other regions is less clear. While Moquegua is more intensively studied than other portions of the south-central Andes, the strong Tiwanaku presence appears to reflect a real Tiwanaku focus on the region. Large Tiwanaku residential sites as well as cemeteries are reported for the Caplina, Sama, and Locumba valleys but have not been fully described (Baitzel and Rivera Infante, 2019; Mujica et al., 1983; Muñoz Ovalle and Gordillo Begazo, 2016; Vela, 1992). Despite sizable Tiwanaku cemeteries in the Azapa Valley, few and relatively small Tiwanaku settlements have been found, suggesting very modest colonial enclaves amongst local populations or no direct colonial presence (Goldstein, 1995; Korpisaari et al., 2014). Contemporaneous Tiwanaku-affiliated materials in northern Chilean valleys are typically interpreted as instances of cultural emulation and indirect influence, without direct biological or economic colonization (Augustyniak, 2004; Torres-Rouff et al., 2015; Uribe, 2004).

Tiwanaku-related styles such as Tumilaca and Cabuza emerged locally in the Moquegua, Locumba, Sama, Caplina, and Azapa valleys. These cultural developments do not appear to originate with Tiwanaku's initial hegemonic expansion, but rather reflect a secondary dispersal of highland and interandean Tiwanaku populations under socio-political duress as the state collapsed late in the Middle Horizon (Korpisaari et al., 2014; Owen, 2005; Owen and Goldstein, 2001; Sharratt, 2016; Sims, 2006).

The complexity of Tiwanaku influence indicates that people, commodities, and ideas moved through both direct and indirect connections. The variability of these networks represents an important debate regarding the development of the archaic state. At issue are how absolute control may have been within a Titicaca-littoral Tiwanaku "heartland", whether territorial control extended to direct colonies in the Pacific coastal valleys, and if Tiwanaku influence elsewhere throughout the southern Central Andes in fact represent secondary settlements and exchange networks. Sociopolitical, logistical, and ecological factors likely were important constraining factors in shaping Tiwanaku networks. Here, we focus on the potential role that ecological resources may have had in facilitating or hindering the establishment of Tiwanaku transportation corridors, contributing to the various networking strategies the state employed.

2.2. *Long distance caravan trade in Andean states*

Archaeological evidence and analogy with ethnohistorical records indicate that long-distance transport of commodities by camelid caravans was likely the primary mode of Tiwanaku migrations (Browman, 1974; Dillehay and Núñez, 1988; Mujica et al., 1983; Nielsen, 2001; Núñez and Dillehay, 1979; Stanish et al., 2010; Tripcevich, 2016). Caravan-based exchange has been a necessity in the Andean region to ensure the biological and social health of pastoral communities, as well as their herds. Specialized highland Andean pastoralism, such as that described ethnographically by Flores Ochoa (1979) and Flannery et al. (1989), runs the risk of nutritional deficiencies. To offset this, specialized pastoralists acquire cereals, tubers, legumes, vegetables, and fruits through trade with lower-altitude agriculturalists (Flannery et al., 1989; Flores Ochoa, 1979; Orlove, 1981). Andean herders require alcohol, coca, ritual paraphernalia, and foodstuffs for social and ritual occasions (Flannery et al., 1989), while caravans and migration are vital opportunities for information and cultural exchange (Nielsen, 2001). Additionally, long-distance exchange of elite, exotic, and high-value goods is linked with emergent social differentiation in the Andean Formative and Middle Horizon (Goldstein, 2000; Nielsen, 2013; Tripcevich, 2010), as it is in other regions globally (Algaze, 1993; Hirth, 1996; Smith, 1990).

Ethnoarchaeological and ethnohistoric accounts provide much information on the organization of Andean caravan trade (De la Vega, 1966; Gil Montero, 2004; Nielsen, 2001, 1997; Tripcevich, 2016). By most descriptions, average-sized caravans number 15–20 animals while larger ones contain 40–50. Caravans smaller than 15 animals are generally not considered worthwhile, while practical constraints limit the upper size of caravans to 100–120 animals. *Arrieros* in Potosi state that caravans larger than this are divided into separate, optimally-sized droves, with additional drovers, in order to manage the animals and accommodate limited pasturage and other resources found en route (Nielsen, 2001, p. 168).

Even larger, formal state caravans were essential during the Inka and Colonial periods to transport products that financed military, political, ecclesiastical, and mining operations. Garcilosa de la Vega describes state-sponsored Inka military trains numbering in the thousands of animals (1966, p. 515). Zárate estimates one Inka military train at 15,000 animals, driven by approximately 40–50 drovers (cited in Flannery et al., 1989, p. 114). Historical documents describe large caravans and intense activity along corridors connecting colonial Arequipa (including Moquegua) with highland mining communities. 18th century mortgages from Moquegua record purchases of "*carneros de la tierra*" that carried immense volumes of produce and alcohol to Chucuito and Potosí in caravans numbering between 150 and 700 animals. Inventories of alcohol that originated in Moquegua and was consumed at Potosi (Rice, 1997) provide an indication of the total volume of traffic. Using standardarized *botija* (jar) volumes and llama and mule load capacities (Rice, 1997; Rice and Ruhl, 1989), approximately 27,700 ($\pm$6403, 1 σ) llamas or 6500 ($\pm$1494, 1 σ) mules per annum traveled between Moquegua and the Chucuito during 1778–1795, the period of peak consumption at Potosi.

We hypothesize that comparably high volumes of traffic occurred during the Tiwanaku period. Currently, the evidence for Tiwanaku caravans is largely indirect, and consists of osteological markers for robust camelids hypothesized to have been pack animals, traded commodities, and portions of road networks (Browman, 1975, 1974; Dillehay and Núñez, 1988; Gasco and Marsh, 2015; Núñez and Dillehay, 1979; Tripcevich, 2010; Vallières, 2016). Stable and radiogenic isotopes indicate a majority of camelids consumed in lowland sites and at Tiwanaku originated in highland environments (Thornton et al., 2011; Vallières, 2016; c.f., Knudson et al., 2012; Mader et al., 2018 for supporting evidence from other periods). Cumulatively, there is evidence for large volumes of camelids in the highlands, both as transient pack animals as well as endemic herds yielding products for consumption at Tiwanaku related sites.

Such large animal cohorts had a human accompaniment. Multiple descriptions of ethnographic and ethnohistoric caravans yield an estimate of approximately one drover, or *arriero*, per every 12 llamas in a caravan (Browman, 1974; Cobo, 1990, p. 367; Flannery et al., 1989, p. 115; Warthon Blancas, 1995). Additionally, bioarchaeological evidence documents frequent bidirectional demic movement associated with Middle Horizon caravans, as both ethnically Tiwanaku and non-Tiwanaku individuals moved between Tiwanaku, direct colonial enclaves in Moquegua, and other culturally-affiliated communities (Baitzel and Goldstein, 2016; Blom et al., 1997; Knudson et al., 2004, 2014; Knudson, 2008; Torres-Rouff et al., 2015).

The increasing frequency and magnitude of mobility as well as a greater demand for camelid products during the Middle Horizon likely represents a significant pressure on highland ecological resources (Vining, 2016; Vining and Burns, 2018). Unlike many examples of pastoralism where limited resources conditioned nomadic mobility (Chang and Koster, 1994; Khazanov, 1994), prehistoric and recent herding in the central Andes is characterized by relative sedentism, labor investments to expand and improve territorially-circumscribed pastures and regular residential and economic mobility between established pasturing territories and trading partners (Dransart, 2002; Flannery et al., 1989; Flores Ochoa, 1979; Gil Montero, 2004; Lane, 2006; Nielsen, 2001; Orlove, 1981, 1977; Palacios Ríos, 1988, 1977; Tomka, 2001; Tripcevich, 2016).

Such relatively fixed mobility circuits and pasturing territories represent a significant cumulative pressure on Andean highlands ecological resources. The pronounced topography of Andean montane environments likely further served to channel movements into fewer, well-established and preferential paths, enhancing pressure on particular vegetation resources along established routes. Such ecological anisotropy likely was an important factor that shaped the development of long distance trade and migration during the Andean Middle Horizon. Further, preferential pressures on these environmental affordances may have become embedded recursively in the long-term ecological and socio-political development of the region.

2.3. General vegetation and camelid ecology

A comprehensive discussion of seasonal vegetation dynamics within the ROI and how these relate to pastoral ecology is provided inVining (2016) and Vining and Burns (2018). Here, this information is summarized. Vegetation cover in the study area is affected by regional orographic rainfall gradients and ranges from bare (interAndean desert valleys and adjacent highlands), to sparse (within a high elevation belt above approximately 3500 masl), to moderately dense (along the Titicaca littoral). Marked seasonal and interannual differences in precipitation further effect moisture availability and, ultimately, vegetation. Meteoric precipitation decreases dramatically between the dry – wet seasons. Within the Suches – Mazo Cruz corridor, mean wet season (DJF) precipitation for the period 1954–2008 is 90.7 mm, while mean dry season (JJA) precipitation is only 3.1 mm (Fig. 2). Further, interannual wet season precipitation is highly variable and, during dry years, wet-season monthly precipitation may approximate normal dry season amounts (Fig. 2).

In response to precipitation, green vegetation contracts greatly from maximum wet season conditions to a dry season minimum by late September. By late October–November, early austral spring precipitation begins and green vegetation quickly recovers. Consequently, green vegetation minima during August – late September is an ecological limitation that constrains intensive camelid grazing by either endemic herds or transient caravans.

Four major vegetation communities characterize the high-elevation regions through which Tiwanaku caravans traveled: wetlands (*bofedales*), two types of grasslands (*pajonales* and *césped de la puna*), and mixed grass-shrub communities (*tolares*). Dispersed bunchgrass (*Festuca* sp. and *Stipa* sp.) and/or low shrubs (*Parastrephia* sp.) are the most extensive communities, but are the sparsest vegetation cover and provide the lowest quality pasture for camelids. In contrast, high-elevation-adapted wetlands comprising dense growth of Juncaceae and Cyperaceae with grasses, Asteraceae, and other forbs (Fonkén, 2014; Heiser, 1978; Pulgar Vidal, 1979; Soukup, 1970; Tosi, 1960) are relatively discrete vegetation patches that provide the most reliable and highest quality feed for camelids. Wetland vegetation communities are vital to Andean pastoralism.

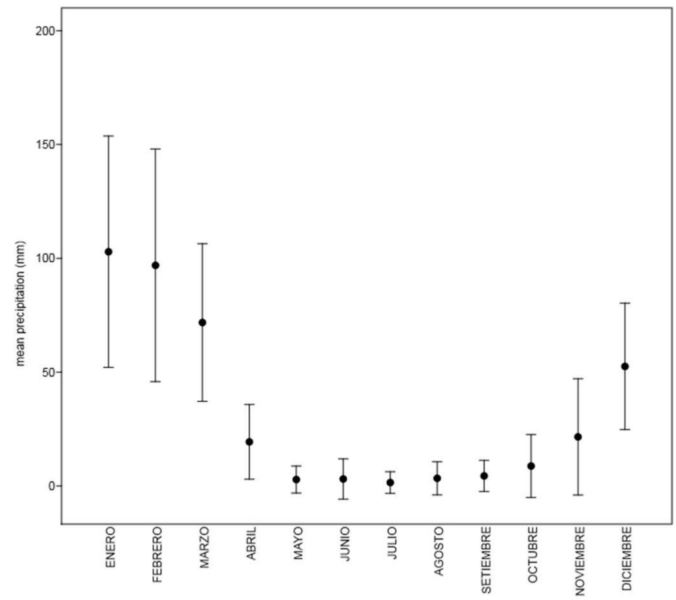

Fig. 2. Mean monthly precipitation accumulations and standard deviation recorded at Lake Suches (70° 24′ 12″ W, 16° 55′ 35″ S). Data are provided by Southern Peru Copper Corporation and Proyecto Pasto Grande.

Botanical analysis of Andean camelid diets indicates that alpacas are relative dietary specialists while llamas have broader dietary breadth. The greatest dietary diversity is indicated for llamas in non-highland environments, reflecting foddering of penned animals as well as dietary opportunism (DeNiro, 1988; Finucane et al., 2006; Shimada and Shimada, 1985). While pastured, both camelid species rely on grasses, forbs, and other vascular species found in high-elevation wetlands (*bofedales* or *vegas*) or grasslands (Bryant and Farfan, 1984; Castellaro et al., 2004; Reiner and Bryant, 1986). Depending on vegetation productivity, pastured camelids require between 0.58 and 9.17 ha/animal for sustained grazing (Vining, 2011: table 4.7). Alpacas are intensively grazed on highly-productive wetland pastures and represent the lower end of this spectrum. Llamas, which will browse opportunistically on lower quality vegetation, represent the higher end. Notwithstanding evidence of penned foddering, the distribution of suitable high-elevation pastures—wetland vegetation for alpacas and both wetlands and *pajonales* for llamas—strongly influences the geographic distribution of Andean camelids (Flannery et al., 1989; Kuznar, 1991a, 1991b; Tomka, 2001). Consequently, access to productive and reliable grazing that is sufficient to support both small individual caravans and larger state-sponsored caravans described ethnohistorically represents an important constraint on Andean mobility circuits.

3. Methods

3.1. Locating Tiwanaku sites

The locations of archaeological sites related to Tiwanaku's colonial expansions were identified from published literature (Table 1). Precise coordinates were available for Tiwanaku sites in the Moquegua/Osmore drainage; the Suches – Mazo Cruz region; and the Wankarani, Tiwanaku

Valley, Katari Basin, and Taraco Peninsula survey regions (Albarracin-Jordan and Mathews, 1990; Bandy, 2001; Janusek and Kolata, 2003; McAndrews, 2005; Owen and Goldstein, 2001; Stanish et al., 2010; Vining, 2011). The Tiwanaku site at San Antonio de Locumba was located using in-situ GPS measurements taken in 2004. Obsidian from the Chivay source is the most prevalent in Tiwanaku-affiliated sites (Burger et al., 2000; Glascock and Giesso, 2012) and GPS coordinates for one source are incorporated into our model of Tiwanaku transport routes (Tripcevich, 2010, 2007). However, Tiwanuku occupations have yet to be recorded at Chivay despite prior surveys around the obsidian sources, and current models suggest down-the-line exchange rather than direct procurement may be the best model for how this resource was exploited by Tiwanaku (Doutriaux, 2004; Tripcevich and MacKay, 2011).

For other Tiwanaku sites, precise coordinate data have not been published. Tiwanaku sites in Arequipa were identified by Cardona Rosas (2010) and their locations reconstructed from open-sourced imagery. Tiwanaku-related sites in the Sama, Caplina, and Azapa Valleys were also approximated from the coordinates of modern toponyms cross-referenced with the approximate locations indicated on small-scale published maps (Baitzel and Rivera Infante, 2019; Goldstein, 1995; Muñoz Ovalle and Gordillo Begazo, 2016; Vela, 1992). Similar approaches were used to relocate Tiwanaku sites in the southern Titicaca/Desaguadero region (Bennett, 1950; Pärssinen, 2005; Smith and Janusek, 2014). Tiwanaku sites in the Juli-Pomata and Ccapia-Desaguadero surveys reported by Stanish et al. (1997) were located by digitizing published maps. The last two approaches are significantly less precise than reconstructing locations from published coordinates, but in lieu of such data, the accuracy is sufficient at our regional scale of analysis. As our objective is to model movement between the urban center of Tiwanaku and its principal areas of activity in the western Pacific Valleys, we focus on Tiwanaku sites in Moquegua, Locumba and Caplina, Arequipa, and Chivay. Other Tiwanaku sites are provided for illustrative purposes.

3.2. Estimating cost-paths and mobility corridors

There is substantial discussion concerning best practices for modeling short to long distance archaeological movements while accurately factoring physiogeographic or energetic considerations, travel time and scheduling, economic interests, foraging patterns, social networks, or a constellation of such constraints (Douglas, 1994; Frachetti et al., 2017; Howey, 2011, 2007; Kohut, 2018; Llobera et al., 2011; Taliaferro et al., 2010; Tripcevich, 2016; Wernke, 2012; White and Surface-Evans, 2012). The merits of each method often can be found in how it weighs different permutations of these factors and the importance of global versus localized knowledge in determining paths of movement.

In modeling Tiwakanu migration and caravan routes, we take as basic assumptions that 1) principal paths of movement had been established during earlier cultural periods and global knowledge regarding origins, destinations and the landscapes in between was available and 2) at a regional scale, the highly mountainous topography of the central Andes was the principal constraint on movement. Conventional least-cost paths (LCP), particularly ones constrained by topographic cost-surfaces, are suitable given these assumptions as they rely on global knowledge to determine routes of minimal friction between identified starting and end-points (Douglas, 1994). Given the dramatic topographic relief of the Andes at a regional scale, the assumption that topography heavily influenced paths of movement is reasonable. Stanish et al. (2010) used LCP modeling to approximate transportation routes between Tiwanaku and Moquegua; the analysis we present here is an extension of that approach.

As topography is a main constraint on regional movement, slope was the principal input in determining cost surfaces. Non-void filled Shuttle Radar Topography Mission (SRTM) 3-arc second (approximately 90 m) digital terrain data (NASA-JPL, 2013) were void-filled with cubic convolution resampling and mosaicked to cover the study region. Slope in degrees was derived from the resulting digital terrain model (DTM) using standard functions in ESRI ArcGIS (ArcInfo 10.4.1). For least-cost analysis, the slope product was reclassified into twenty classes representing increasing friction and mobility costs from least (1) to greatest (20) as slope increases. Additionally, there are several large water bodies within the area of interest. Watercraft were almost certainly used to navigate near-shore areas of Lake Titicaca. Significant water transport on smaller water bodies in the Andean highlands and/or involving camelids is unlikely. Consequently these represent impediments to camelid caravans and drovers that would need to have been circumnavigated. To reflect this, water bodies over 30 ha in surface area were categorized as twice as costly to transit as the greatest slope. The resulting cost parameters were combined linearly with raster-based mathematic operations into a single cost surface. Pair-wise least cost paths between Tiwanaku and inter-Andean and Western valley destinations were subsequently calculated following standard ArcGIS LCP processes, and the resulting paths vectorized.

Recent archaeological critiques of LCP approaches emphasize the role of contingent decision-making which takes into account multiple criteria and/or multiple possible pathways (e.g., Howey, 2011, 2007), or the role of impedence factors in influencing multidirectional movements rather than movement between discrete starting and end-points (Kohut, 2018). Howey (2007) notes that multiple factors affect relative movement costs, including slope, waterways (as transport), and landcover. Our LCP analysis estimates mobility costs constrained by two of these factors. Densely-forested landcover as described by Howey is not a factor in the study region. Other factors, including pasture resources and trading partners, are important determinants for Andean caravan routes. However, as we are testing vegetation dynamics between destinations, these factors are not incorporated into our mobility models as variables.

Howey (2011)further notes that decision-making and landscape

Table 1
Locations of Tiwanaku sites used in modeling mobility corridors.

Site	Datum	Latitude (DD)	Longitude (DD)	Cultural affiliation	Valley/ region	source
Tiwanaku	WGS 84	−16.545169	−68.671977	Tiwanaku	Tiwanaku	Albarracin Jordan and Mathews (1990)
Chivay	WGS 84	−15.62729	−71.518248	obsidian source	Arequipa	Tripcevich (2007)
Socabaya	WGS 84	−16.460085	−71.527692	Tiwanaku	Arequipa	Cardona Rosas (1997)
Kasapatac	WGS 84	−16.43593	−71.559914	Tiwanaku cemetery	Arequipa	Cardona Rosas (1997)
San Antonio de Locumba	WGS 84	−17.609578	−70.751886	Late Tiwanaku	Locumba	Field mapped
Omo	WGS 84	−17.232212	−70.977707	Tiwanaku	Osmore	Goldstein and Owen (2001)
Chen Chen	WGS 84	−17.184146	−70.921838	Tiwanaku	Osmore	Goldstein and Owen (2001)
Loreto Viejo	WGS 84	−17.604167	−71.233055	post Tiwanaku/Tumilaca	Osmore	Owen and Goldstein (2001)
Tocuco	WGS 84	- 17.840833	- 70.11417	Late Tiwanaku	Caplina	Mujica et al. (1983)
Magollo	WGS 84	- 18.033755	- 70.266891	Late Tiwanaku	Caplina	Muñoz Ovalle and Gordillo Begazo (2016)
Parra	WGS 84	- 18.108626	- 70.407856	Late Tiwanaku	Caplina	Vela (1992), Muñoz Ovalle and Gordillo Begazo (2016)
El Atajo	WGS 84	- 18.108226	- 70.405967	Late Tiwanaku	Caplina	Vela (1992), Muñoz Ovalle and Gordillo Begazo (2016)
Azapa/Alto Ramirez	WGS 84	- 18.523109	- 70.165900	Late Tiwanaku	Azapa	Goldstein (1995)

conditions are subject to change, and multiple pathways may be used to accommodate these contingencies. The topographic factors that we evaluate in the LCP model regionally have been relatively stable since the Tiwanaku period. The well-documented arid phase linked with Tiwanaku collapse changed regional hydrology ca. AD 1000–1300 (Abbott et al., 1997; Baker et al., 2009; Binford et al., 1997; Thompson et al., 1985). It resulted in a 10–12 m draw-down of Lake Titicaca's southern subbasin (Lago Wiñaymarka) only after ca. AD 1200, however (Abbott et al., 1997). Due to Wiñaymarka's basin morphology, this potentially shifted transportation corridors only 5 km northwards from the current lake outlet at Desaguadero. Paleolimnological reconstructions for other small lakes in the region (Abbott et al., 2003; Baker et al., 2009) suggest open water conditions during the Tiwanaku period. Pollen spectra indicate similar vegetation regimes from ca. 3100 BP – present (Paduano et al., 2003).

Given that motivations for Tiwanaku migrations were highly variable and reasonably could have resulted in multi-criteria/multi-pathway mobility, we evaluated the LCP models against a circuit-theory or "permeability" approach (Howey, 2011; c.f., Kohut, 2018 who evaluates movement as a function of "affordances"). Circuit theory is based on the premise that landscape features will variably impede (resist) or facilitate (conduct) all types of movements, whether directed, semi-directed or random-walk. Connectivity between two locations is a function of an intermediate terrain of resistors and conductors, and multiple routes through this terrain may present equally viable paths between origins and destinations.

To evaluate how LCP and circuit-based models of Tiwanaku mobility differ, we modeled landscape permeability using Circuitscape 4.0 software. Circuitscape is designed for modeling connectivity in conservation ecology (McRae et al., 2008), with applications to archaeological cases (Howey, 2011). The terrain-based cost surface used for LCP modeling was input as landscape 'resistance' in Circuitscape, and both pairwise- and cumulative resistance surfaces were calculated for all Tiwanaku sites listed in Table 1. The resulting cumulative resistance surface is compared to the LCP analysis in Fig. 3. This landscape permeability model can be used to inform interpretations of prehispanic mobility by itself. We further used this as the input to derive permeability-based LCPs.

The results of conventional LCP and permeability-based LCP analyses are compared in Fig. 4. While both approaches yielded comparable results, there are enough minor deviations to suggest Tiwanaku mobility did not depend on a single "path". This is corroborated by archaeological sites in the Mazo Cruz – Suches region. Tiwanaku caravan sites are found up to 8 km from paths predicted by regional criteria, suggesting decisions made locally to navigate conditions encountered during movement resulted in multiple alternate path segments. Consequently, we model Tiwanaku transportation routes as corridors, expanding outwards from modeled paths for up to 20 km on either side. Such corridors encapsulate all segments of probable Tiwanaku paths recorded between Mazo Cruz and Suches; result in mutually-exclusive corridors leading to each destination discussed here; and cover the majority of our ROI in order to evaluate relationships between regional ecological dynamics and likely migration corridors.

3.3. Remote sensing of highland vegetation

We model highland vegetation productivity from multispectral images acquired by the Landsat 5 Thematic Mapper (TM) and Landsat 7 Enhanced Thematic Mapper (ETM+) satellites (Table 2, Fig. 5). The imagery used was acquired between 1975 and 2009. These images overlap with instrumental data recorded by meteorological stations at Lake Suches and Pasto Grande from 1954 to 2008. Images were processed in Harris Geospatial Environment for Visualizing Imagery (ENVI 4.7) and ArcGIS software. Visible – shortwave infrared bands (Table 2) were layer-stacked and resampled to 30 m resolution. Each scene was geometrically corrected to an orthorectified Landsat base image acquired on Sept 21, 1990 using a minimum of 30 ground-control points per scene (2nd order polynomial nearest-neighbor transformation with a mean RMS error = 24.3). Scenes were radiometrically corrected by dark-object subtraction, using image values from deep water bodies for band minima.

Vegetated landcover was mapped through two approaches: First, we generated a regional estimate of vegetation dry-season minima from an image segmentation of mosaicked Landsat 'Tasseled Cap' transforms (TC) covering the entire ROI. This estimate of vegetation minima represents limiting constraints on pasturage available to both endemic herds and caravans. Second, we estimated interdecadal vegetation variation within a subset of the study region covering the area between Desaguadero and Asana, Peru from a time-series of soil-adjusted vegetation indices (SAVI). This subset corresponds to a stretch of probable caravan routes between Tiwanaku and its colonies at Omo and Chen-Chen (Stanish et al., 2010; Vining, 2011).

3.3.1. Regional vegetation minima

Four scenes (Table 3) acquired during the austral winter were used to generate a cloud-free mosaic that captures the minimal distribution of perennial vegetation throughout the study region (Fig. 6). These images date from August 1999–July 2001 and represent average to slightly

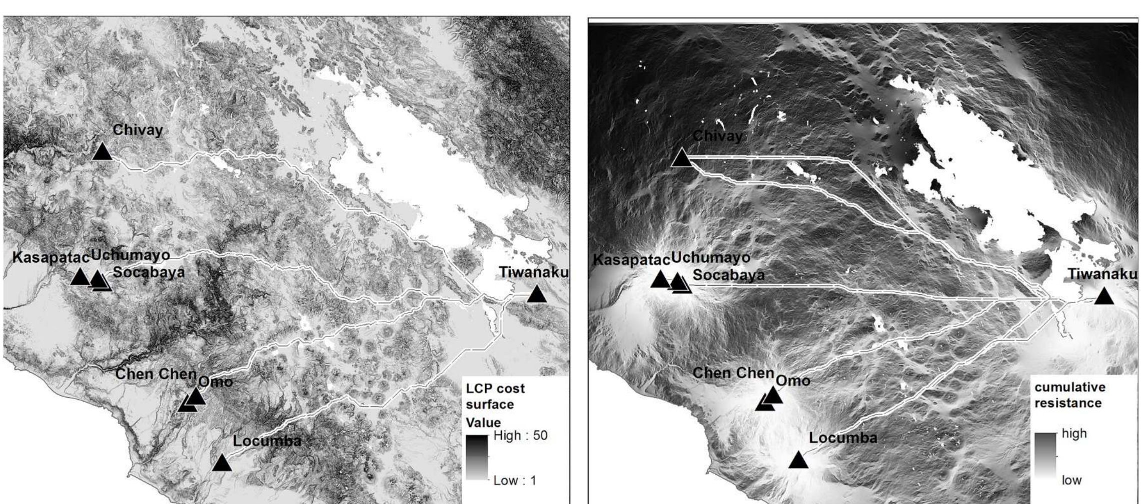

Fig. 3. Comparison of least-cost surfaces (left) and omni-directional permeability surfaces (right), and the respective least-cost paths calculated from each.

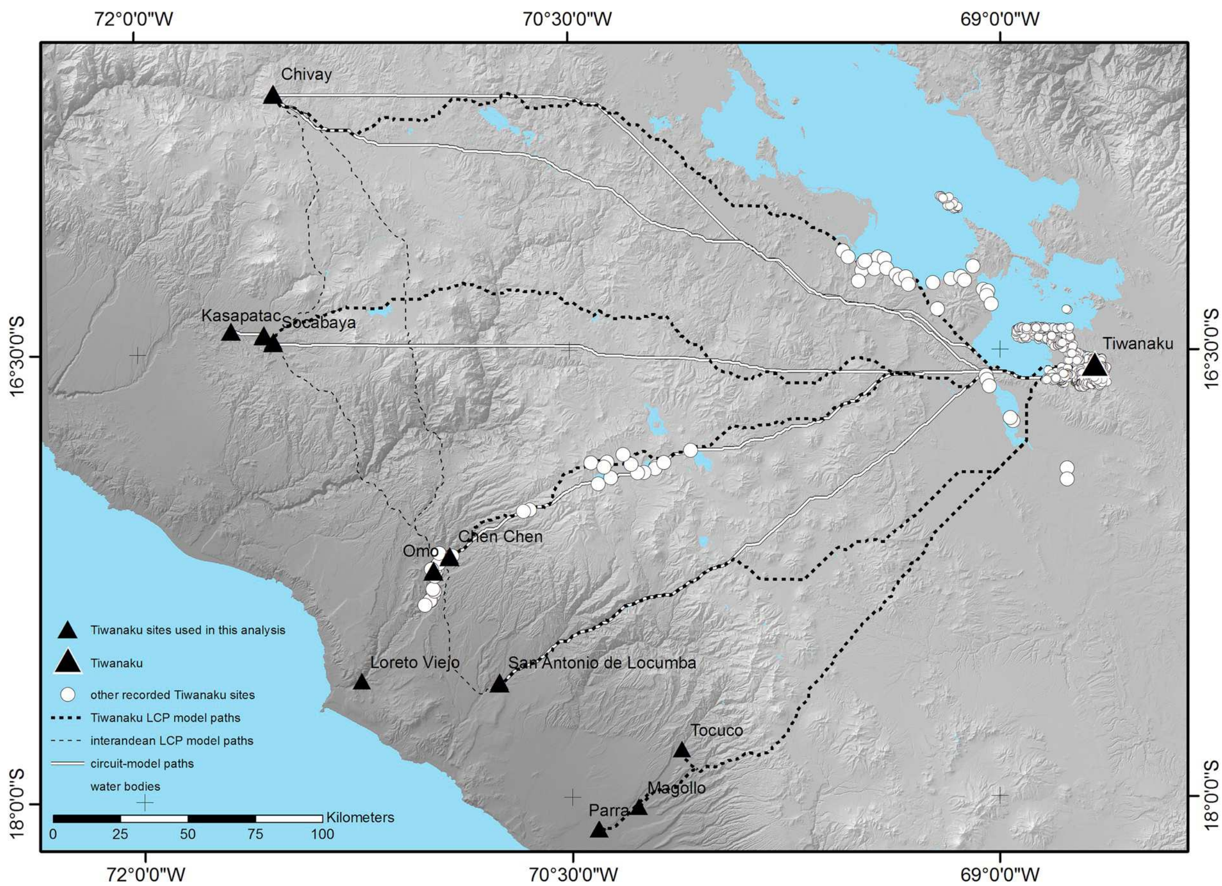

Fig. 4. The derived paths showing their relationships to documented Tiwanaku sites in the southern Titicaca and Pacific Valley regions.

Table 2
Landsat platforms and band orders used in this analysis.

Platform/sensor	Bands	Wavelength (μM)	Resolution (M)
Landsat 4 Multispectral Scanner (MSS)	Band 1 - Green	0.5–0.6	60
	Band 2 - Red	0.6–0.7	60
	Band 3 - Near Infrared (NIR)	0.7–0.8	60
	Band 4 - Near Infrared (NIR)	0.8–1.1	60
Landsat 5 Thematic Mapper (TM)	Band 1 - Blue	0.45–0.52	30
	Band 2 - Green	0.52–0.60	30
	Band 3 - Red	0.63–0.69	30
	Band 4 - Near Infrared (NIR)	0.76–0.90	30
	Band 5 - Shortwave Infrared (SWIR) 1	1.55–1.75	30
	Band 6 - Thermal	10.40–12.50	120
	Band 7 - Shortwave Infrared (SWIR) 2	2.08–2.35	30
Landsat 7 Enhanced Thematic Mapper (ETM+)	Band 1 - Blue	0.45–0.52	30
	Band 2 - Green	0.52–0.60	30
	Band 3 - Red	0.63–0.69	30
	Band 4 - Near Infrared (NIR)	0.77–0.90	30
	Band 5 - Shortwave Infrared (SWIR) 1	1.55–1.75	30
	Band 6 - Thermal	10.40–12.50	60
	Band 7 - Shortwave Infrared (SWIR) 2	2.09–2.35	30
	Band 8 - Panchromatic	.52–.90	15

wetter than average dry season conditions, the period during which instrumental and remote sensing data overlap. Despite the multi-year coverage of the mosaic, the selected scenes reflect similar vegetation responses to available moisture. They further were acquired under similar solar illumination conditions, facilitating landcover mapping.

Minimal green vegetation cover was estimated using the Tassled Cap (TC) transform designed for Landsat sensors (Crist and Cicone, 1984; Huang et al., 2002). TC is a physically-based multispectral data transform that captures up to 95% of within-image variability in two data planes and can be used to directly observe differences in soil, vegetation, and moisture conditions. The TC-transform creates three products useful for assessing fractional vegetation, soil, and transitional soil – vegetation cover: Brightness (the weighted sum of total reflectance); Greenness (derived from vegetation's high absorption in the visible range and high reflectance in the NIR range); and Wetness (a function of greater mid – shortwave infrared absorption with increasing water content) (Crist and Cicone, 1984). Brightness and Wetness together define bare soil, Greenness correlates with vegetation cover, and Wetness defines

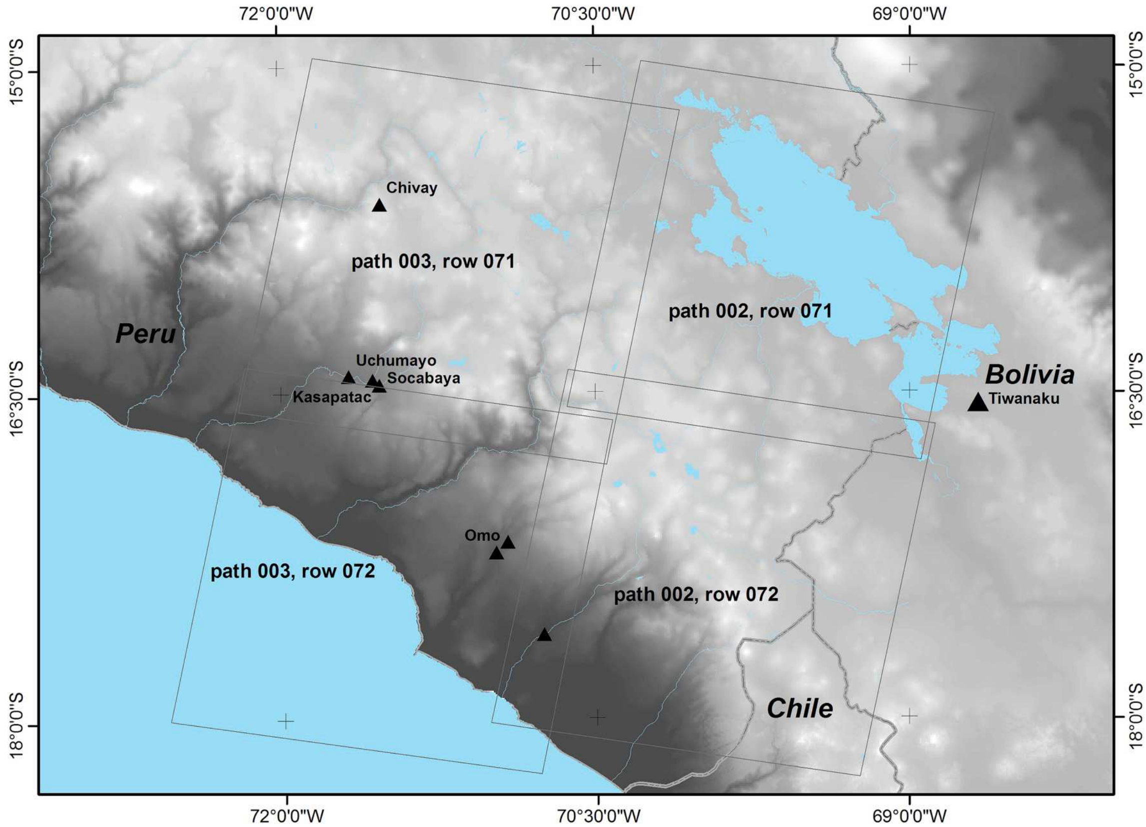

Fig. 5. Index of Landsat scenes used for vegetation analysis.

Table 3
List of Landsat scenes and acquisition dates used in this analysis. TSA indicates scenes used in time-series analysis. TC indicates scenes used to derive Tassle-Cap components.

Scene ID	Platform	sensor	Path	Row	Acquisition date	Approx. scene center	application
p001r72_2m19750622	Landsat 4	MSS	001	072	1975-06-22	Candarave	TSA
p002r72_5t19870113	Landsat 5	TM	002	072	1987-01-13	Candarave	TSA
p002r72_5t19900921	Landsat 5	TM	002	072	1990-09-21	Candarave	TSA
L71002072_07219990802	Landsat 5	TM	002	072	1999-08-02	Candarave	TSA
L71002072_07219991106	Landsat 7	ETM+	002	072	1999-11-06	Candarave	TSA
p002r072_7t20000414	Landsat 7	ETM+	002	072	2000-04-14	Candarave	TSA
L71002072_07220010401	Landsat 7	ETM+	002	072	2001-04-01	Candarave	TSA
L71002072_07220020810	Landsat 7	ETM+	002	072	2002-08-10	Candarave	TSA
L71002072_07220030525	Landsat 7	ETM+	002	072	2003-05-25	Candarave	TSA
L71002072_07220050802	Landsat 7	ETM+	002	072	2005-08-02	Candarave	TSA
L71002072_07220090423	Landsat 7	ETM+	002	072	2009-04-23	Candarave	TSA
LE70020721999246CUB00	Landsat 7	ETM+	002	072	1999-09-03	Candarave	TSA, TC-mosaic
LE70030712000272EDC00	Landsat 7	ETM+	003	071	2000-09-28	Chivay	TC-mosaic
LE70030721999237EDC00	Landsat 7	ETM+	003	072	1999-08-25	Tambo	TC-mosaic
L7CPF20010701_20010930	Landsat 7	ETM+	002	071	2001-07-22	Lake Titicaca	TC-mosaic

plant/soil moisture content.

A mosaic of minimal vegetation cover was derived by segmenting the TC Greenness (TC-G) component at thresholds that define different classes of green vegetation. In the absence of verifying *in situ* the extent of vegetation land cover during the 1999–2001 period, firsthand knowledge of the Suches basin (approximately in the center of the ROI) was used to set appropriate thresholds to differentiate wetlands and grassland vegetation communities from each other and from bare soils. These regions were further segmented into a binary classification representing green vegetation (TC-G ≥ -55) and non-green landcover that includes water, bare soil/rock, and senescent vegetation. The resulting model of minimal green vegetation cover under dry season conditions is shown in Fig. 6.

3.3.2. *Vegetation time series analysis*

Seasonal to interannual effects on green vegetation were assessed using a time-series of SAVI images. The SAVI time-series covers the period 1975–2009 was calculated from 12 Landsat path 002, row 072 images. These images cover the SE quarter of the ROI between Desaguadero and Asana, Peru. This corresponds to the corridor connecting Tiwanaku to Omo and Chen Chen and to well-documented Colonial era road networks connecting Moquegua with Juli-Pomata and Puno (Rice, 2009, 1997; Stanish et al., 2010; Vining, 2011).

High-quality images with maximum cloud coverage of 1% were used for the time-series analysis (TSA). Due to the need to minimize atmospheric moisture effects in vegetation analyses, the scenes cluster between April–November. These months represent a period of low

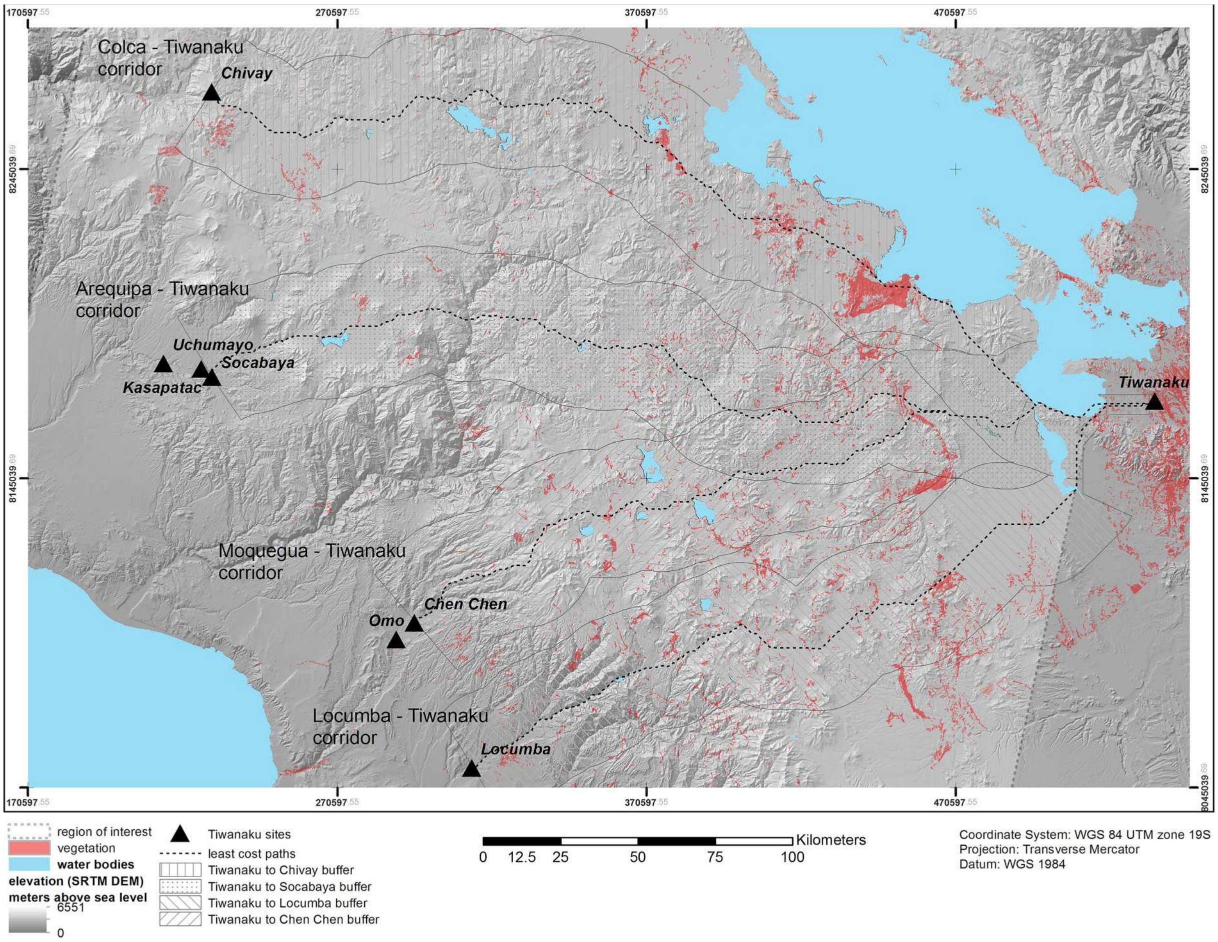

Fig. 6. Minimal perennially-green vegetation land cover in study region showing its relationship to the modeled mobility corridors and Tiwanaku sites.

precipitation following the austral summer DJF wet season (Vining et al., 2019). The pronounced wet- and dry-season climate of the central Andes causes dramatic seasonal differences in the quantity and quality of green vegetation available for pasture (Castellaro et al., 2004; Vining, 2016). Imagery taken between April–November captures a full range of vegetation productivity from peak post-wet season greenness to late dry season senescence, without interference from wet season atmospheric moisture. The time-series further captures variation due to peak interannual dry (1990, 2003) and wet (1999–2000) years, with mesic conditions represented during other years. This time series consequently allows us to evaluate the relative stability of different vegetation communities in response to both seasonal and interannual variations in precipitation.

In regions of sparse – moderate vegetation cover, underlying soils contribute significantly to overall surface reflectance. This is particularly problematic in the red – near infrared (NIR) spectrum. This spectrum is critical for differentiating subtle differences in vegetation photosynthetic activity. However, soil and vegetation lines converge in this spectrum and subtle differences in vegetation productivity can be obscured by soil reflectance (Huete, 1988). Consequently, a number of modified or soil-adjusted vegetation indices are proposed to control for soil-reflectance under partial canopy conditions. Here, we apply the soil-adjusted vegetation index, or SAVI (Huete, 1988; Qi et al., 1994). SAVI is given as:

$$SAVI = 1 + L\left(\frac{\rho NIR - \rho \text{Red}}{\rho NIR + \rho \text{Red} + L}\right) \tag{1}$$

where L is a soil constant ranging between 0 and 1. The factor $(1 + L)$ produces data ranges $(-1$ to $+1)$ similar to the more commonly use normalized-difference vegetation index (NDVI). Optimal soil adjustment factors vary depending on vegetation cover. Higher adjustment values $(L = 1)$ are appropriate for no – low vegetation cover, but these conditions obviate a VI; a value of $L = 0$ assumes complete vegetation canopies and returns the same results as standard NDVI. An L factor tailored to variable soil lines is ideal for regional analyses. In lieu of this, Huete proposed $L = 0.5$, while Qi et al. find a constant of $L = 0.8$ reduces soil noise significantly throughout a range of intermediate vegetation conditions (Huete, 1988; Qi et al., 1994).

Between-images SAVI variance was calculated for the complete time-series as:

$$\sigma^2 SAVI = \frac{\sum (X - \mu)^2}{N} \tag{2}$$

The resulting variance image (Fig. 7) evaluates the relative stability of vegetation communities in response to seasonal and decadal flux in atmospheric moisture. Assuming similar relationships between vegetation growth and past hydroclimate, SAVI variance provides a rough approximation of how stable or predictable discrete vegetation patches may have been during the Tiwanaku period. It also highlights differences in the seasonal behavior of *bofedal* communities, versus grasslands and mixed grass-shrub communities (see below).

4. Results and discussion

4.1. Modeled paths and corridors

Probable paths and migration corridors were modeled between Tiwanaku and known Tiwanaku-related sites in the western Pacific

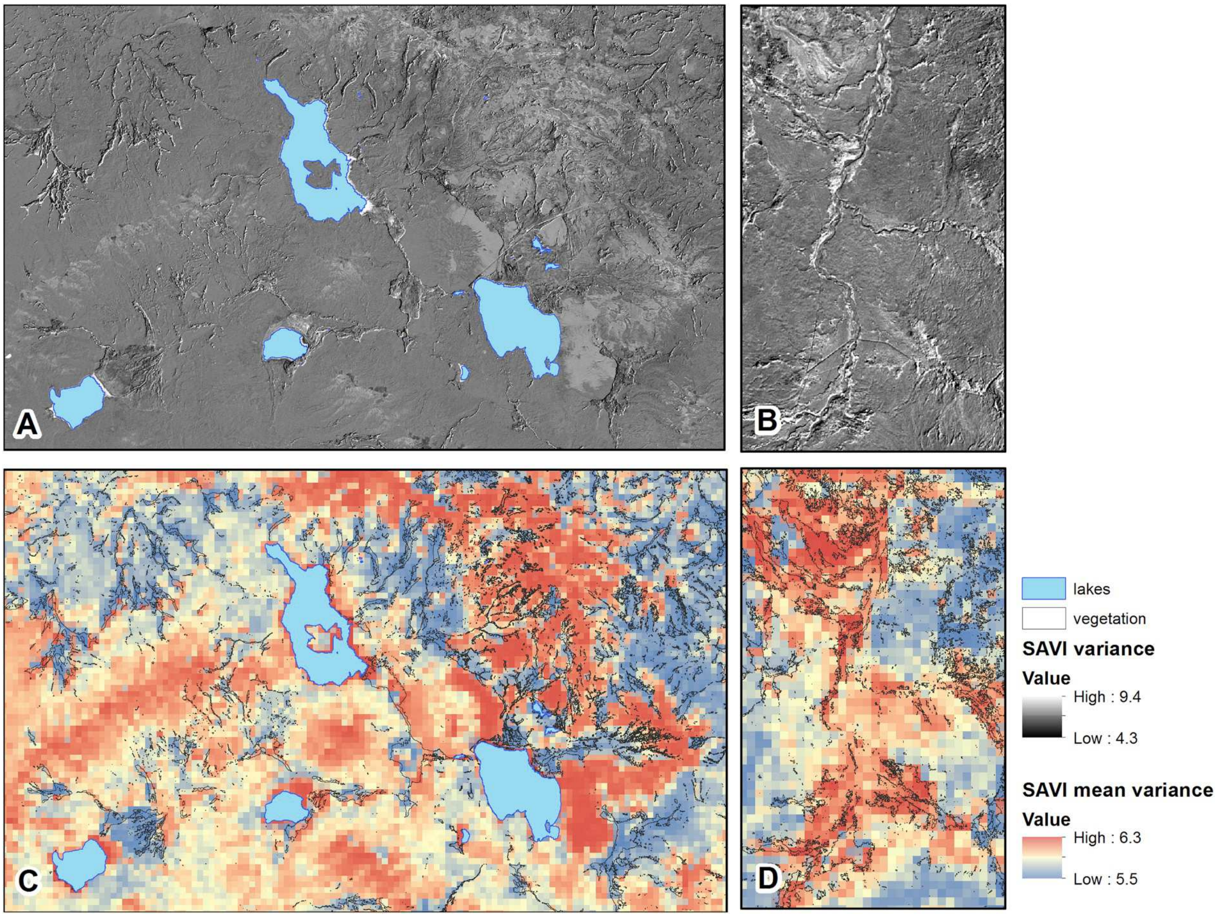

Fig. 7. Variance images for the soil-adjusted vegetation index (SAVI) time series. (A) The region of extensive wetlands in the Suches region is compared to grasslands in the Rio Huenque region (B). The average variance within 500 m neighborhoods shows that the wetlands (C) have much lower inter-annual variance while grasslands (D) show high variance. Vegetation patches are outlined in black.

Valleys. Despite emphasizing different mobility behaviors, LCP and permeability models estimated similar paths between Tiwanaku and its affiliated sites (Figs. 3 and 4). This is likely due to the strong influence topography has on movement, particularly high elevation gradients along the Andean escarpment at the edge of the Altiplano. At the scales of analysis used here, permeability models (Fig. 3B) do not appear to accurately capture very high local travel costs, causing paths to be 'flattened'. This is most apparent in the permeability-based LCP between Tiwanaku and Kasapatac/Socabaya, which does not deviate to accommodate the rugged terrain of the upper Tambo Valley. Portions of the permeability-model LCPs leading to Chivay and San Antonio de Locumba are similarly flattened in ways that are insensitive to local terrain.

Despite this shortcoming, paths modeled from cost-surface and permeability surface LCPs are similar enough that all fall within the corridors we use here to evaluate relationships with landcover (Figs. 4 and 6). As we rely on buffers around estimated paths to approximate corridors of Tiwanaku movement, the minor deviations in the paths estimated by cost-surface and permeability models are less significant. Ethnohistoric caravan networks were flexible according to scheduling, trading, or ecological concerns; thus we think it more likely that migrations occurred within habitually-utilized corridors rather than along any single path. Thus, while we cannot currently evaluate whether Tiwanaku mobility is more accurately replicated by cost- or permeability-based models, we are confident that Tiwanaku migrations occurred within the modeled corridors.

Recorded Tiwanaku sites coincide with the corridors we model here. Tiwanaku-related sites have been recorded in close proximity to the modeled path linking Tiwanaku and Chen Chen (Cardona Rosas, 1997; Stanish et al., 2010; Vining, 2011). Stanish et al. (2010) used modeled Tiwanaku routes to establish their judgmental sample. The other two surveys were regional projects not explicitly focused on identifying Tiwanaku transit corridors. These located Tiwanaku sites both immediately along the modeled route and along segments of alternate routes up to 8 kms away. A similar pattern can be observed in the Juli-Pomata and Desaguadero regions, where modeled paths leading to Chivay coincide with Tiwanaku sites along the Titicaca littoral. The close association between modeled migration routes and recorded Tiwanaku sites, as well as the lack of Tiwanaku sites further away, suggests that Tiwanaku residential mobility and caravanning was largely constrained to corridors centered on the modeled paths.

Our analysis captures flexibility in selecting any particular route by using 20 km wide buffers on either side of the modeled paths. While a multitude of specific path segments were likely used by Tiwanaku migrants, any movement between the site of Tiwanaku and its cultural enclaves or trading partners in the Pacific region would be contained within the respective corridor. The modeled corridors, cumulatively, account for approximately 44% of the area of interest (Fig. 6). With the exception of the eastern portion of the ROI where paths converge on Tiwanaku, the modeled corridors are exclusive of one another. Thus, vegetation within each corridor reflects the availability of pastures exclusive to each potential route.

Both corridor length and total vegetation land cover decrease monotonically from north to south (Table 4). The longer corridor lengths are a function of Tiwanaku's location in the southern Titicaca Basin—accessing valleys north of the Tambo requires circumnavigating

Table 4
Land Cover metrics.

corridor	corridor length (km)	rescaled path length	corridor area (ha)	vegetation area (ha)	total area (ha)	% non-green vegetation	% green vegetation	ratio
Chivay	379.69	1.51	1.11E+06	6.46E+04	1.18E+06	94.52	5.48	1.44
Socabaya	357.57	1.42	1.17E+06	4.03E+04	1.21E+06	96.68	3.32	0.93
Moquegua	288.16	1.14	9.15E+05	3.62E+04	9.51E+05	96.19	3.81	1.32
Locumba	287.16	1.14	9.60E+05	1.77E+04	9.78E+05	98.19	1.81	0.63
Caplina	252.05	1.00	1.04E+06	8.29E+03	1.05E+06	99.21	0.79	0.31

Table 5
Biomass yield and carrying capacities of perennially-green vegetation within modeled mobility corridors.

corridor	days to travel, min	days to travel, max	rest days, min	rest days, max	total travel days, min	total travel days, max	feed requirements RT, min (kg/ llama)	feed requirements RT, max (kg/ llama)	dry biomass yield (kg)	max number camelids	min number camelids
Chivay	17.9	25.1	5.0	4.5	22.9	29.6	102.8	132.4	1.20E+08	1,168,043.9	906,927.4
Socabaya	16.9	23.6	4.7	4.2	21.6	27.8	96.8	124.7	7.50E+07	774,318.9	601,219.7
ChenChen	13.6	19.0	3.8	3.4	17.4	22.4	78.0	100.5	6.73E+07	862,975.0	670,056.7
Locumba	13.6	19.0	3.8	3.4	17.4	22.4	77.8	100.1	3.29E+07	423,698.8	328,980.8
Caplina	11.9	16.6	3.3	3.0	15.2	19.6	68.3	87.9	1.54E+07	226,035.7	175,505.4

the Lake Titicaca shoreline—and the NW – SE trend of the Andean cordillera. As a consequence, greater stretches of the western Altiplano must be traversed to reach Chivay and sites in the Arequipa region. Conversely, the shortest paths connect Tiwanaku to Locumba and Caplina, the southernmost valleys discussed here. Based on average travel rates of 15–20 km per day (Tripcevich, 2010), llama caravans likely required approximately 2–4 weeks, including rest days, to make a one-way trip between Tiwanaku and each destination examined here (Table 5). Llamas on central Andean pastures require approximately 2.25 kg of dry matter per day (Castellaro et al., 2004). With an estimated travel time of approximately 17–22 days for caravans between Tiwanaku – Moquegua (Table 5), a single llama would require 80–100 kgs of feed to complete a roundtrip journey. Pasture en route consequently is an important logistical concern.

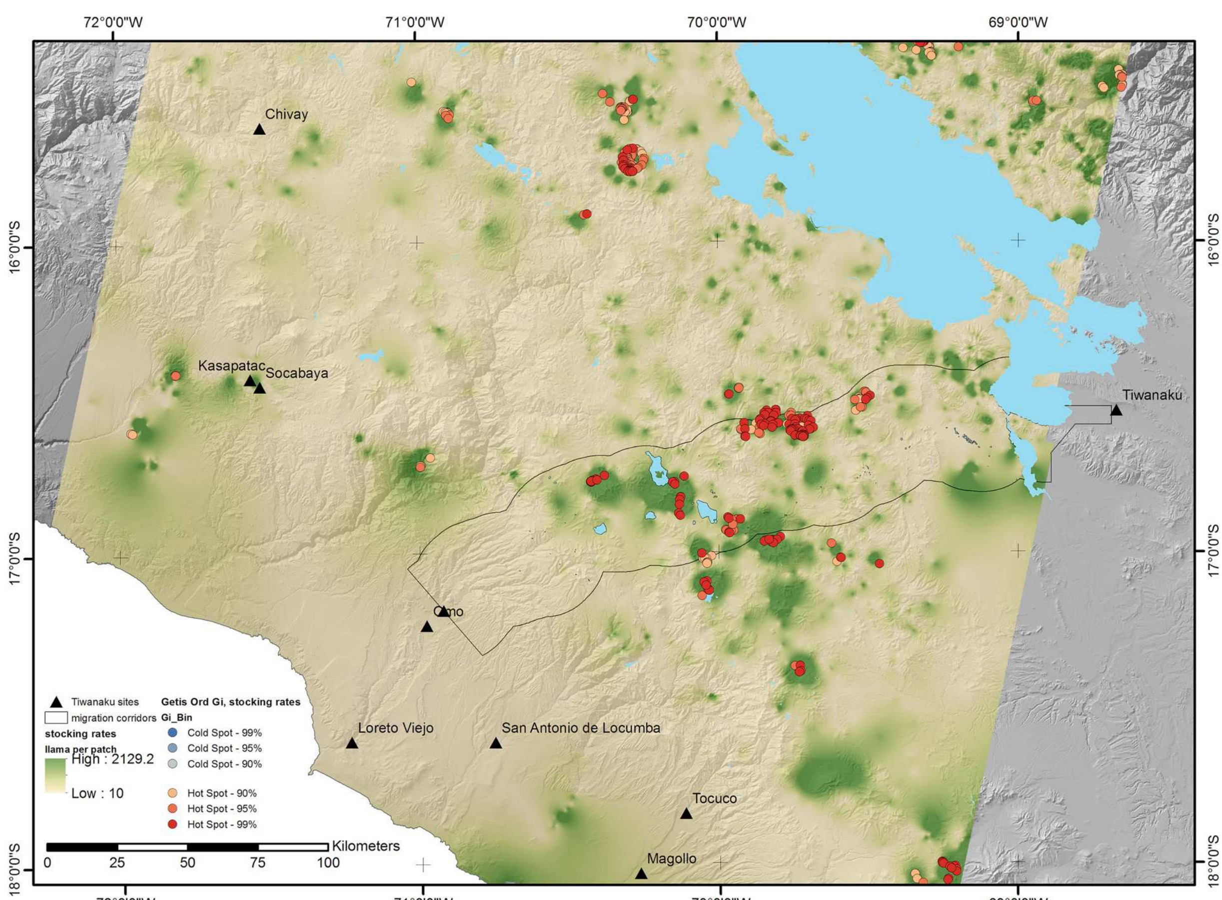

Fig. 8. Estimated llama stocking rates per vegetation patch in the study region, based on information in Vining (2016). Patches with statistically-significant higher z-scores (>2 σ) are shown in red. (For interpretation of the references to colour in this figure legend, the reader is referred to the Web version of this article.)

4.2. Vegetation land cover

Perennially green (i.e., throughout the dry season) vegetation minimally represents an estimated 3.12E+05 ha, or approximately 2.64% of the entire ROI. This estimate is on par with that of Kuznar (1995, p. 36), who estimates *bofedal* coverage in the central Andean area at 2.5%. As noted above, vegetated land cover is most extensive in the northern part of the study region and decreases southwards. This is due to regional moisture gradients and is a recognized factor influencing pastoral ecology (Kuznar, 1991a). The high vegetation cover in the Tiwanaku – Chivay corridor is also due to the fact that much of the path runs along the Titicaca shoreline, with extensive vegetation cover near the Bay of Puno and Lago Umayo. However, vegetation land cover decreases precipitously in the last 100 km of the Chivay path as it crosses the Altiplano.

The western Altiplano above Moquegua and Locumba presents an exception to the southward trend of decreasing vegetation cover. Within the Tiwanaku – Moquegua corridor, there is a dramatic increase in perennially green vegetation to 3.8% of land cover (Table 4; see also Vining, 2011). There is a statistically-significant increase in the size and abundance of *bofedal* wetlands within the Tiwanaku – Moquegua corridor, causing the greater perennially-green land cover (Figs. 8 and 9). *Bofedales* are particularly extensive east of Desaguadero and between Suches – Mazo Cruz (where they approximate 6% of land cover).

With the exception of the Titicaca-littoral portions of the Chivay corridor, the Moquegua corridor further has the highest ratio of green vegetation cover to path length (Table 4, Fig. 9). The vegetation cover/corridor length ratio for Moquegua is more than 4.25 times that of the Caplina corridor; more than double that of the Locumba corridor; and more than 1.4 times that of the Socabaya corridor. Consequently, more green vegetation is available to caravans throughout a trip's duration within the Moquegua corridor than is available along other routes.

Bofedales provide optimal pasturage for camelids, with greater quantities of palatable biomass and higher protein content (Bryant and Farfan, 1984; Castellaro et al., 2004; Reiner and Bryant, 1986). Using estimated stocking rates for both alpacas and llamas on Andean vegetation communities (Vining, 2016: table 7.4), this area could have supported the highest density of camelids within the ROI (Fig. 8). Not only are patches of green vegetation larger and more ubiquitous, the quality of pasturage enables much higher than average densities of camelids to be pastured. Elsewhere, Vining has argued that the availability of high quality pasturage enabled intensified alpaca herding during the Tiwanaku period (Vining, 2016; Vining and Burns, 2018). The availability of high quality pasturage in the Suches –Mazo Cruz area exceeds estimated needs for alpaca herding or llama caravans alone and suggests that both more intensive wool production as well as migrations could have been supported.

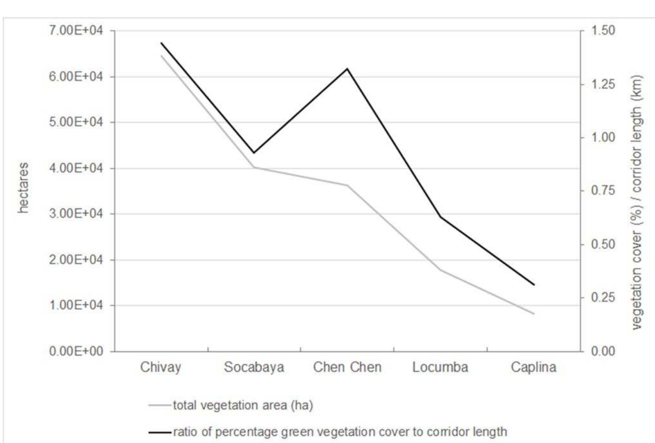

Fig. 9. Comparison of total green vegetation land cover per corridor to land cover as a ratio of corridor length.

4.3. Seasonality and the scheduling of Tiwanaku migrations

SAVI time series analysis reveals an additional factor of vegetation permanence that potentially influenced the magnitude and frequency of Tiwanaku mobility. SAVI analysis reveals the greater sensitivity of grasslands to seasonal and interannual moisture variations, while perennially green vegetation persists in wetlands (Fig. 7). Vegetation around Lakes Suches, Pasto Grande, Vizcachas, and Loriscota is dominated by *bofedal* wetlands and has low variance (Fig. 7A and C). In contrast, vegetation in the nearby Huenque River valley is dominated by bunchgrasses. Bunchgrass communities exhibit high variance, despite being in a similar climatic regime and elevational setting (Fig. 7B and D). While wetland pastures are approximately 63% less productive during the dry season than during the wet season, non-wetland pastures lose productivity almost entirely. Similarly, grasslands are more sensitive to inter-annual variations in moisture, while wetlands sustain more green growth during arid years.

Ethnohistoric information reveals the importance of reliable vegetation resources for sustaining caravan-based mobility. In combination with socioeconomic factors, a recent multi-year drought and loss of available pasture *en route* contributed to a decline in llama caravan traffic in northern Argentina (Vilá, 2018). This example underscores that green pasturage is an important logistical concern for caravan organization. We expect Tiwanaku caravans confronted similar pasturage constraints when scheduling trips. Wetlands provide crucial green vegetation buffers during the dry season and interannual decreases in precipitation.

This has implications for the amount and quality of pasturage available to camelids during different times of the year and during dry climates. Llamas at Parinacota (Chile) were found to diversify their diets during the wet season, when *Festuca* and *Stipa* -dominated grasslands green and become attractive pastures (Castellaro et al., 2004). Conversely llamas' dietary diversity decreases during the dry season and they rely on wetland pastures as other vegetation senesces. The availability of wetland pasturage facilitates dry-season mobility, while senescent non-wetland vegetation limits it.

Several socio-ecological factors intersect to influence the seasonal scheduling of llama-based caravans and trading activity (Casaverde, 1977; Nielsen, 2009, 1997; Rabey et al., 1986; Tripcevich, 2010, 2007). Many of these factors foster more frequent caravans during the drier months between the austral fall – winter. Rabey et al. (1986) note two periods of *ferias* in the dry Puna (northern Chile, Argentina, and southern Bolivia). The first occurs in March–April, when recently-harvested, "fresh" agricultural products (fruits, vegetables, and meat/wool) are abundant. The second occurs between late August and October, when dried or produced goods (textiles, leather, *charki*, or conserved agricultural products) are traded. Nielsen (1997) offers that caravans are timed to arrive after agricultural harvests, when agricultural labor is not needed, harvested goods are available for trade, and arriving caravan animals will not threaten agricultural fields before they are harvested. Pasture quality also determines when meat animals are most fit for slaughter and when caravans can anticipate finding quality pasturage *en route*. Removing animals for the caravans during the dry season also alleviates grazing pressures on home pastures (Nielsen, 2001, p. 170).

While ethnohistoric information on caravan scheduling is based on the dry Puna, seasonal moisture and temperature differences operate as a similar constraint within our ROI. Peak demands for agricultural labor in the Titicaca basin occur during the austral summer wet season, between late November and May. Labor demands are highest in November–December during planting, and during harvesting in late May–June prior to austral winter temperature lows (Bandy, 2005, p. 288). This leaves the period of June–November for Tiwanaku caravans, assuming they accommodated similar agricultural calendars. Peak dry season vegetation conditions—namely decreased green vegetation availability and poorer pasture quality—occur during this window, from June–September. As a consequence, perennially-green wetland vegetation provides scheduling flexibility for Tiwanaku migrations, facilitating migrations and trading trips during the critical dry season. Where wetland cover is lesser, mobility had less scheduling flexibility and may have relied on wet season grasslands. This creates the potential for scheduling conflicts between caravans and other agropastoral cycles.

5. Conclusion

While archaeological research has long standing interest in migration and long distance trade, less attention has been dedicated to the ecological context that facilitates or perhaps even may result from preferential paths of residential and economic mobility. Geospatial modeling allows us to predict several paths that articulated urban Tiwanaku with affiliated satellite communities throughout the south-central Andes. In the case of the Tiwanaku – Moquegua corridor, we have direct archaeological evidence corroborating the use of this route by Tiwanaku migrants and this invites future investigation to evaluate the possible use of similar corridors during the Middle Horizon.

Remote sensing of vegetation productivity, focusing on green-vegetation minima during the central Andean dry season, reveals a statistically significant increase in perennially-green vegetation land cover and a corridor linking urban Tiwanaku with its principal economic and ethnic enclaves in Moquegua. This corridor shows the highest ratio of path length/perennial green vegetation in the south-central Andes. Wetlands within this corridor are more extensive than the average for adjacent Altiplano regions. Further, they are more stable than adjacent communities despite seasonal – decadal variations in precipitation. Estimated stocking rates for these communities suggest that large number of camelids could have been supported, particularly during the dry season when senescent vegetation presents a limiting constraint on mobility elsewhere in the central Andes. The abundance of perennially green vegetation along the route linking Tiwanaku to Moquegua likely was an important resource for camelid caravans, which enabled high volumes of traffic between Tiwanaku and its colonial satellites.

The relationship between the extensive wetlands in the Tiwanaku – Moquegua corridor and migration is a matter that merits further examination. Macro-regional ecological dynamics may have played a role in the distribution of Tiwanaku influence, by providing preferentially-distributed affordances that facilitated or complicated caravan mobility. However, whether the prevalence of perennially-green vegetation is a natural condition that was capitalized upon when long-distance connections between the Titicaca Basin and the Pacific coast were established, or if this is in part a product of these connections, is undetermined. In the case of the former scenario, naturally-occurring wetlands near the Desaguadero and Mazo Cruz – Suches regions may have reduced risks associated with caravanning, permitted greater flexibility in scheduling demic and economic mobility, allowed Tiwanaku to have sustained transportation networks during adverse climatic phases, and ultimately contributed to the establishment of Tiwanaku's most important colonies in Moquegua.

Alternately, Niche Construction theory (Laland and O'Brien, 2010; Smith, 2011; Zeder, 2016) raises the intriguing possibility that increased human pressure on wetlands at the start of the Middle Horizon, both from pastoral production and migrations, may have contributed to the enhancement of preexisting natural wetlands. Domesticated camelids have preferential diets and place selective pressures on wetland plants (Castellaro et al., 2004; Reiner and Bryant, 1986). Grasses and herbaceous vegetation tends to be suppressed by these pressures, encouraging the growth of cushion plants that in turn promote wetland health. At a minimum, intensified wetland grazing by resident camelid herds, which dates at least as early as the Middle Horizon (Vining, 2016; Vining and Burns, 2018), likely increased selective grazing pressures and contributed to wetland development.

The direct, deliberate anthropogenic modification of these wetlands is also plausible. Contemporary Andean herders improve and expand pastures by controlling animals, redirecting water, and burning vegetation to encourage different species (Palacios Ríos, 1988, 1977; Verzijl and Quispe, 2013). Similar anthropogenic enhancements of *bofedal* wetlands in Ancash and northern Chile have been dated to the Middle Horizon (Domic et al., 2018; Lane, 2009). Non-*bofedal* wetlands in the Titicaca basin were modified for agricultural and pastoral activities beginning in the Tiwanaku period (Erickson, 2000, 1992; Janusek and Kolata, 2004; Stanish, 1994). In a positive feedback loop, the initial attraction of wetland environments may have encouraged subsequent intervention by pastoralists and caravans to 'improve' camelid pastures, contributing to the overall growth and enhancement of these environments.

Geospatial modeling of Tiwanaku mobility networks and vegetation dynamics suggests that the ecology context of the western Altiplano had a role, in tandem with socio-economic factors, in fostering Tiwanaku long distance trade and migration in the prehispanic world. The unusual structure of vegetation communities along the transportation network linking Tiwanaku to its main Moquegua colonies raises the possibility that Tiwanaku mobility could have had a significant role in shaping the contemporary Andean environment, with effects that persist into recent periods.

Authors contributions

The research problem presented here was conceptualized by PRW. The research method, data collection, and analysis were designed and executed by BRV. BRV wrote the manuscript with support from PRW. All authors reviewed the final manuscript.

Declaration of competing interest

None.

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