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PERSPECTIVE

Variation in reciprocal subsidies between lakes and land: perspectives from the mountains of California[1]

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Abstract: Lakes are connected to surrounding terrestrial habitats by reciprocal flows of energy and nutrients. We synthesize data from California's mountain lake catchments to investigate how these reciprocal subsidies change along an elevational gradient and with the introduction of a top aquatic predator. At lower elevations, well-developed terrestrial vegetation provides relatively large inputs of organic material to lakes, whereas at higher elevations, the paucity of terrestrial vegetation provides minimal organic input but allows for higher inputs of inorganic nitrogen. There are also pronounced elevational patterns in amphibians and aquatic insects, which represent important vectors for resource flows from lakes back to land. The introduction of trout can reduce this lake-to-land resource transfer, as trout consume amphibians and aquatic insects. We propose a conceptual model in which within-lake processes influence terrestrial consumers at higher elevations, while terrestrial inputs govern within-lake processes at lower elevations. This model contributes to a more general understanding of the connections between aquatic and terrestrial habitats in complex landscapes.

Résumé : Les lacs sont reliés aux habitats terrestres qui les entourent par des flux réciproques d'énergie et de nutriments. Nous mettons en rapport des données tirées de bassins versants de lacs de montagne en Californie pour étudier les variations de ces apports réciproques le long d'un gradient altitudinal et après l'introduction d'un prédateur aquatique de niveau trophique supérieur. À basse altitude, une végétation terrestre bien développée fournit de relativement grands apports de matière organique aux lacs, alors qu'à plus haute altitude, la rareté de la végétation terrestre fournit peu d'apports organiques, mais permet des apports d'azote inorganique plus importants. Des variations altitudinales marquées sont également observées chez les amphibiens et les insectes aquatiques, qui représentent d'importants vecteurs pour les flux de ressources des lacs vers la terre. L'introduction de truites peut réduire ce transfert de ressources des lacs vers la terre, puisque les truites consomment des amphibiens et des insectes aquatiques. Nous proposons un modèle conceptuel dans lequel les processus internes des lacs influencent les consommateurs terrestres à plus haute altitude, alors que les apports terrestres régissent les processus internes des lacs de plus basse altitude. Ce modèle participe à une compréhension plus générale des liens entre les habitats aquatiques et terrestres dans des paysages complexes. [Traduit par la Rédaction]

Introduction

The transport of energy and resources across habitat boundaries has important consequences for food-web dynamics and ecosystem function (Polis et al. 1997, 2004; Loreau et al. 2003; Richardson and Sato 2015). Most studies of cross-ecosystem resource subsidies have focused on a single direction of resource flow, e.g., the transport of terrestrial organic matter into aquatic ecosystems (Caraco and Cole 2004). However, resources frequently move in both directions across habitat boundaries, and these reciprocal linkages can play an important role in determining the trophic structure of landscapes (Nakano and Murakami 2001; Baxter et al. 2004; Leroux and Loreau 2011). Among the best studied cross-boundary resource flows are those between lakes and their surrounding catchments (Cole et al. 1994, 2011; del Giorgio et al. 1999; Prairie et al. 2002; Gratton et al. 2008; Gratton and Vander Zanden 2009). However, reciprocal linkages between lakes and land have largely been studied in isolation from each other (Vander Zanden and Gratton 2011), which hampers efforts to forge a more holistic understanding of the dynamical interdependence of these linked aquatic and terrestrial systems.

Terrestrial inputs exert a number of fundamental controls on the structure and function of aquatic ecosystems. The overall level of primary and secondary production that a lake supports is largely determined by nutrient concentrations (Naumann 1919; Carlson 1977) that, in turn, are often dependent on watershed sources (Odum 1969; Hutchinson 1970). In addition to nutrients such as nitrogen and phosphorous, organic carbon has emerged as a second principal axis governing aquatic ecosystems (Williamson et al. 1999). Terrestrially derived organic carbon can influence lake ecosystem function by acting as a metabolic substrate for heterotrophic microorganisms (del Giorgio and Peters 1994; Pace et al. 2004), often leading to rates of ecosystem respiration that are higher than primary production, resulting in net ecosystem heterotrophy (Prairie et al. 2002; Hanson

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et al. 2003). Although terrestrial inputs of organic materials also support higher level consumers in both benthic (Hershey et al. 2006; Solomon et al. 2011) and pelagic (Vander Zanden et al. 2006; Francis and Schindler 2009; Cole et al. 2011) habitats, this effect can be weak (Brett et al. 2009; Francis et al. 2011; Mehner et al. 2015) and the factors that determine the extent to which terrestrial resources support aquatic consumers remain poorly understood.

For most lakes, the total amount of energy and resources transferred from the lake to the surrounding terrestrial habitats is likely to be dwarfed by terrestrial inputs to the lake (Vander Zanden and Gratton 2011). However, the resources flowing out of lakes (mostly in the form of animal biomass) tend to be high-quality food items, and aquatic resources can be just as important to terrestrial animals as terrestrial resources are to aquatic animals (Bartels et al. 2012). The emergence of aquatic insects (Gratton and Vander Zanden 2009; Bartrons et al. 2013; Dreyer et al. 2015) and amphibians (Regester et al. 2006; Gibbons et al. 2006; Schriever et al. 2013) are the best studied lake-to-land resource flows, and these subsidies can have important effects on terrestrial ecosystems (Richardson and Sato 2015). For example, changes in consumer density and behavior associated with emerging aquatic insects can have cascading top-down effects on lower trophic levels in riparian areas surrounding streams (Henschel et al. 2001; Murakami and Nakano 2002; Sabo and Power 2002), and the deposition of aquatic insect carcasses can represent an important source of nutrients to terrestrial plants near lakes (Hoekman et al. 2012), with consequent bottom-up effects on higher trophic levels (Bultman et al. 2014).

Although connections between aquatic and terrestrial habitats are clear, ecologists are still working towards understanding the dynamical interdependence of linked aquatic and terrestrial systems. This interdependence manifests itself in both food-web properties (e.g., interaction strengths, feeding behavior) and ecosystem processes (e.g., rates of production and energy flux) (Marcarelli et al. 2011). For example, in a groundbreaking study evaluating reciprocal linkages between streams and surrounding forests, Nakano and Murakami (2001) showed that aquatic insects represent an important fraction of the annual energy budget of forest birds and that terrestrial insects play a similar role for fish. These reciprocal resource subsidies stabilized consumer communities on both sides of the aquatic–terrestrial boundary, highlighting the importance of evaluating aquatic habitats and surrounding catchments as interlinked ecological units. While there is still relatively little empirical work on reciprocal subsidies (but see Greig et al. 2012; Scharnweber et al. 2014), recent theoretical studies have used the meta-ecosystem framework (Loreau et al. 2003) as a foundation to explore the dynamics of ecosystems linked by reciprocal subsidies. These studies highlight the importance of the magnitude, composition, and timing of reciprocal subsidies in determining the structure and function of linked ecosystems (Gravel et al. 2010; Leroux and Loreau 2011).

The strong gradients in catchment characteristics and climatic variables found in mountainous landscapes provide an excellent opportunity to evaluate the effects of environmental heterogeneity on the magnitude, composition, and timing of reciprocal subsidies. In this paper, we synthesize data from previously published work and ongoing projects to formulate a conceptual model describing the effects of elevation and introduced trout on cross-ecosystem subsidies between lakes and surrounding catchments in the mountains of California. Our main goal is to assess how catchment and community context influence the role of lakes as hotspots of carbon and nutrient processing and sources of prey in landscapes.

Study system: California's mountain lakes

The mountains of California provide a superb natural laboratory to study lake–land linkages across environmental gradients. Many of California's mountain lakes are found in the Sierra Nevada and Klamath mountain ranges, and lake catchments in these ranges are the focus of our review. The Sierra Nevada and Klamath ranges contain thousands of comparatively small (median size is approximately 2 ha), naturally formed lakes, nearly all of which are glacial in origin and occur at elevations between 1500 and 3500 m. Mountain lakes tend to be oligotrophic and clear-watered, which makes them highly sensitive to even small changes in terrestrial inputs of nutrients or organic matter. Aquatic macrophytes are relatively uncommon (with the exception of sedges in shallow littoral zones), so the base of the aquatic food web is represented mostly by autotrophic and heterotrophic microorganisms (both benthic and pelagic).

Perhaps most importantly from the standpoint of developing a conceptual understanding of reciprocal lake–land resource subsidies, California's mountain lakes and their surrounding catchments are characterized by strong elevation gradients that regulate a number of ecologically important abiotic and biotic factors (Fig. 1). These include elevational gradients in temperature, terrestrial vegetation cover, and soil development. Elevation and catchment characteristics can be broadly used to classify lakes as either high- or low-elevation lakes, with the tree line (2000–2900 m depending on latitude) as a good general delineation between the two. Low-elevation lakes are warmer and generally occur in catchments consisting of mixed coniferous forest with reasonably well-developed soils. In contrast, high-elevation alpine lakes are colder and typically exist in catchments dominated by bare rock, with little vegetation or soil organic matter (Fig. 1). Elevation also has important influences on the duration of the snow-free period, and the proportion of precipitation falling as snow. Elevation is not the only environmental factor that has the potential to influence reciprocal subsidies in California's mountain lakes. For example, lake area and depth have important effects on species composition in Sierra Nevada lakes (Knapp et al. 2001*b*, 2005; Knapp 2005). However, we chose to focus on elevation, as it is the dominant factor regulating catchment characteristics and aquatic communities show strong and consistent responses to elevational gradients (Knapp et al. 2001*b*, 2005; Knapp 2005).

Historically, natural fish barriers prevented fish from colonizing most of California's mountain lakes following the most recent glaciation 10 000 years ago. Despite such natural barriers, the majority of lakes now contain trout (primarily *Salvelinus fontinalis*, *Oncorhynchus mykiss*, and *Salmo trutta*) that were introduced within the last 120 years for recreational angling purposes (Knapp et al. 2001*a*). This creates a patchwork in which most lakes are now occupied by an introduced top predator, while a smaller number exist in their naturally fishless state. Trout have dramatic effects on aquatic communities in California's mountain lakes, and these effects tend to be at least as important as the effects of abiotic environmental variables, if not more so (Knapp et al. 2005; Pope et al. 2009). Because introduced trout have dramatic and robust impacts on factors related to reciprocal lake–land subsidies, we also include fish in our conceptual model.

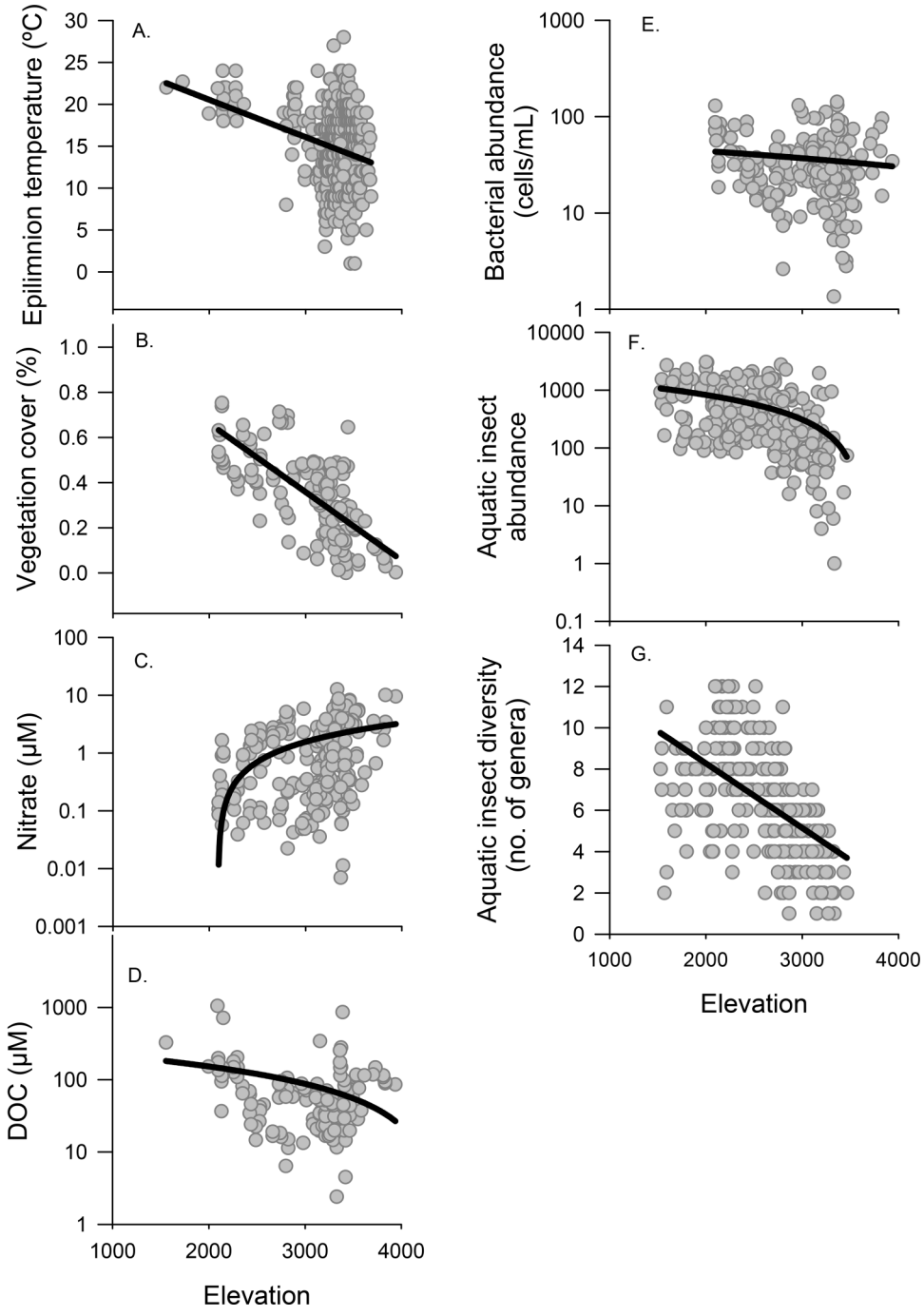
Land-to-lake subsidies

Terrestrial subsidies to California's mountain lakes include both organic matter and inorganic nutrients. Most organic matter is derived from catchment soils and vegetation, while inorganic nutrients tend to be derived from atmospheric deposition and remineralized soil organic pools. Here we focus on hydrologic transport of organic matter and aeolian insect inputs. However, other terrestrial inputs such as coarse particulate organic matter (e.g., pollen from conifer trees) represent substantial, largely unexplored subsidies to California's mountain lakes.

Organic matter

Terrestrial inputs of organic material to California's mountain lakes show distinct seasonal patterns associated with snowmelt-driven hydrology. Nutrient and dissolved organic carbon (DOC) concentrations are typically highest during snowmelt (S. Sadro, unpublished data), when soils are saturated, hydrologic connectivity is high, and rates of biological uptake in lakes and streams are low.

Fig. 1. Elevation is a principal regulator of cross-system subsidies through its control of both biotic and abiotic factors. To demonstrate how these factors vary with elevation, we update and augment previously published data (B–E) and present new analyses (A, F–G). (A) Epilimnetic lake temperature measured between July and August (R^2 = 0.11, N = 389, F = 45.9, p < 0.0001); (B) total percent vegetation cover based on the National Land Cover Database (R^2 = 0.48, N = 222, F = 199.1, p < 0.0001) (Sadro et al. 2012); (C) nitrate concentration (R^2 = 0.12, N = 232, F = 29.7, p < 0.0001) (Sadro et al. 2012); (D) dissolved organic carbon (DOC) concentration (R^2 = 0.10, N = 149, F = 17.1, p < 0.0001) (Sadro et al. 2012); (E) bacterial abundance (R^2 = 0.09, N = 132, F = 13.3, p = 0.0004) (Sadro et al. 2012); (F) biphasic aquatic insect abundance, measured as the total number of individuals collected at each lake in a sample consisting of 15 D-net sweeps 1 m long (R^2 = 0.15, N = 278, F = 47.1, p < 0.0001) (Knapp et al. 2005); and (G) diversity of biphasic aquatic insects, measured as the number of genera present (R^2 = 0.29, N = 278, F = 114.1, p < 0.0001) (Knapp et al. 2005).



The composition of dissolved organic matter (DOM) can be characterized using the fluorescence index (FI), which quantifies the relative proportion of terrestrially derived fulvic acids in the DOM pool (McKnight et al. 2001). FI values are lowest during and immediately after snowmelt, reflecting DOM largely of terrestrial origin; however, over the course of the growing season, the proportion of DOM that comes from terrestrial sources declines — terrestrial DOM fluxes decrease with declining stream flows, increasing water residence time provides greater potential for photooxidation of terrestrial DOM within the water column, and seasonally warming lake waters

support increased rates of primary production that increase the amount of DOM derived from aquatic sources (Nelson 2009; Sadro et al. 2011*a*). However, event-driven fluxes of terrestrial organic matter associated with summer and autumn rain storms (Sadro and Melack 2012) and terrestrial insect swarms (Carlton and Goldman 1984) can be quite high. Seasonal patterns in organic matter fluxes are important because they structure the availability of material in relation to seasonal patterns in lake temperature, water residence time, and overall metabolic activity within lakes.

Strong elevation gradients in soil development and vegetation cover create natural variation in the magnitude of terrestrial material available as inputs (Sadro et al. 2012). Lakes positioned above the tree line drain catchments that are dominated by ice and rock, while lower elevation lakes drain catchments that usually feature large areas of shrub or forest cover (Fig. 1B). The general pattern of increased terrestrial productivity at lower elevations is reflected in both the concentration and composition of DOM in lakes and streams (Fig. 1D). At Sierra Nevada wide spatial scales, vegetation cover accounts for nearly half of the variation found in DOC concentrations (Sadro et al. 2012). The effect is even more pronounced within individual catchments, where increasing vegetation cover can account for up to 90% of the variation in DOC along downstream flow paths. Changes in FI along these downstream gradients within individual catchments indicate a shift in DOM from autochthonous carbon derived from within-lake primary production to terrestrial sources. Much of the unexplained variation in the concentration or composition of DOM along elevation gradients can be attributed to the presence of specific habitat types. In particular, wet meadow or peat soils, which occur across a broad elevation range, leach high concentrations of terrestrial DOM into lakes (S. Sadro, unpublished data).

In addition to the landscape characteristics described above, the flux of organic matter into aquatic ecosystems in the Sierra will depend on hydrological factors that may also vary with elevation. There are few watershed studies in which fluxes are systematically measured along landscape gradients. We can, however, estimate flux amounts using lake DOC concentrations, which are correlated with inlet stream concentrations (S. Sadro, unpublished data). Assuming similarly sized lakes with comparable watersheds, DOC fluxes into high-elevation lakes are expected to be on the order of 0.2 g $C{\cdot}m^{-2}{\cdot}day^{-1}$. DOC fluxes into low-elevation lakes, estimated at 0.7 g $C{\cdot}m^{-2}{\cdot}day^{-1}$, are predicted to be at least three times higher. These estimates are likely to underrepresent fluxes at lower elevation sites, where precipitation is more likely to fall as rain, which tends to mobilize more DOM than melting snow. Although particulate organic matter is likely to be an important carbon source to lakes, at least seasonally, a lack of data from both high- and low-elevation sites in the Sierra Nevada and patterns of mobilization that may be highly variable in time restrict our ability to estimate fluxes.

Inorganic nutrients

In a typical year, half or more of all inorganic nitrogen inputs to Sierra Nevada waters are flushed from catchment soils and talus during snowmelt, with the remainder originating directly from atmospheric deposition to the snowpack (Sickman et al. 2001); isotopic studies have shown that both snowpack- and soil-derived nitrates are found in streams during snowmelt (Sickman et al. 2003*a*). Rain can also be an important nitrogen input to mountain ecosystems (Sadro and Melack 2012). Nitrate concentrations are substantially higher in rainwater than in snow (Williams and Melack 1991), and in years with little overwinter snow accumulation, or with unusually large amounts of precipitation falling as rain, inorganic nitrogen inputs may not follow the typical pattern driven by spring snowmelt hydrodynamics. As runoff from snowmelt or rain infiltrates and flushes the catchment, variability in soil structure and vegetation type plays an important role in nitrogen release. Nutrient release from soils is controlled by the accumulation of litter in the organic horizon (Miller et al. 2005), the influence of snowpack on soil moisture and remineralization rates (Johnson et al. 2009), and the magnitude of plant root development in the O horizon (Johnson et al. 2009). In their review of nutrient cycling in forests of the eastern Sierra Nevada Mountains, Johnson et al. (2009) suggest that very high concentrations of inorganic nitrogen and phosphorus in runoff waters resulted from nutrients mineralized from the soil O horizon that were not taken up by plants and that remained above hydrophobic mineral soils. Catchment vegetation composition can also play a role in determining inorganic nitrogen inputs. For example, streams with flow paths that cross through patches of nitrogen-fixing alders (*Alnus tenuifolia*) carry significant amounts of inorganic nitrogen to Castle Lake, a subalpine lake in the Klamath Mountains (Goldman 1961). Thus, nitrate concentrations in mountain lakes reflect seasonal variability in precipitation source, snowmelt hydrodynamics, vegetation type and soil structure, and rates of biological uptake — concentrations are typically highest early in the season when catchment uptake is low, hydrologic connectivity is high, and internal rates of primary productivity are low (Sickman et al. 2003*a*; Sadro et al. 2011*b*). Although these factors vary somewhat with latitude across California, in general, catchment retention should increase and aquatic concentrations should decrease with declining elevation. Landscape patterns in nitrate concentrations reflect these processes. Nitrate concentrations vary strongly with elevation (Fig. 1C), and lakes in high-elevation catchments that are predominantly rock have the highest concentrations of nitrates (Sadro et al. 2012), both because snowpack deposition is higher at higher elevations and because lower vegetation cover means that less nitrate is taken up by terrestrial sources. A pattern of decline in lake nitrate concentrations along landscape gradients of decreasing rock cover and increasing vegetation cover occurs consistently in catchments throughout the Sierra Nevada (Sadro et al. 2012), reflecting increased terrestrial uptake along an elevation gradient and the likelihood of reduced terrestrial fluxes with decreasing elevation.

In contrast to landscape patterns for nitrogen, concentrations of inorganic phosphorus are uniformly low in Sierra Nevada lakes and show little variation with elevation (Sadro et al. 2012). Catchment inputs are limited by terrestrial uptake and geochemical reactions that bind inorganic phosphorous to aluminum and iron particles in soils (Homyak et al. 2014*a*). Rates of internal loading from lake sediments are also low (Homyak et al. 2014*b*). Despite these constraints on phosphorus fluxes, long-term data from the Sierra Nevada suggest that phosphorus loading has occurred over the last two decades (Sickman et al. 2003*b*), driven primarily by atmospheric deposition (Vicars et al. 2010). The extent to which phosphorus deposition may vary with elevation remains unknown.

The timing and magnitude of inorganic nutrient fluxes into lakes are important to cross-system fluxes in much the same way as organic matter dynamics. Nutrient concentrations are linked to the remineralization of DOM by aquatic microbes and the production of new organic matter by autotrophs, both potentially important pathways of organic matter flux to aquatic consumers. Given the strong elevation-driven gradients in inorganic nitrogen availability, it is likely that food webs of low-elevation lakes will rely on remineralized terrestrial organic matter to a greater extent than those of high-elevation lakes.

Effects of organic matter and inorganic nutrient inputs on aquatic ecosystems

There is strong evidence that terrestrial organic matter and nutrient inputs exert functional control on ecosystem energetics and community structure at the base of the food web in Sierra Nevada lakes. Although widespread studies of lake metabolism are lacking, inferences regarding spatial patterns might be drawn from seasonal variability. Phenological shifts in the importance of terrestrial inputs are evident in lake metabolism studies conducted at Emerald Lake, a relatively high-elevation lake in the southern Sierra Nevada. In a year with little nonwinter precipitation,

heterotrophy tended to occur early in the ice-free season, when rates of primary production were low and the DOM pool was dominated by allochthonous material; in contrast, the lake was autotrophic during the majority of the growing season, during which rates of respiration tended to closely track rates of primary production (Sadro et al. 2011*b*, 2011*c*). These changes in carbon source are reflected in phenological shifts in bacterioplankton community composition — bacterioplankton communities in Emerald Lake closely tracked seasonal changes in DOM source, suggesting that temporal shifts in microbial community structure and lake metabolism are driven in part by bacterioplankton adaptation to changes in DOM composition (Nelson 2009). Event-driven fluxes of terrestrial organic matter can disrupt these seasonal patterns — terrestrial organic matter mobilized by summer and autumn rain storms can be high enough to decouple bacterioplankton metabolism from autotrophic production, ultimately causing a temporary shift in ecosystem metabolism toward heterotrophy (Sadro and Melack 2012). Assuming that the majority of metabolic activity occurs during the ice-free season, mean annual metabolic carbon fluxes in this high-elevation lake were 0.7 g C·m^{-2}·day^{-1} for gross primary production and 0.6 g C·m^{-2}·day^{-1} for respiration. As a result, net ecosystem production was a slightly positive 0.09 g C·m^{-2}·day^{-1} and carbon cycling within the lake was in near equilibrium.

The interplay between internal rates of primary production and terrestrial loading of organic matter is also evident at the landscape scale. Bacterioplankton abundance in Sierra Nevada lakes increases along downstream flow paths (Fig. 1E) in conjunction with increasing terrestrial vegetation in catchments, increasing DOC concentration, and DOM composition that reflects increasingly allochthonous sources (Sadro et al. 2012); these changes are strongly correlated with differences in bacterial community composition between headwater and downstream lakes (Nelson et al. 2009). Primary productivity in lakes also appears to increase with decreasing elevation. Chlorophyll *a* concentrations, a proxy for productivity, are variable but tend to be lower in high-elevation lakes (S. Sadro and J. Sickman, unpublished data), likely because phytoplankton growth is limited by low water temperatures and the brevity of the growing season. While terrestrial nutrient inputs are likely to be highest at high-elevation lakes, climatic conditions limit the capacity of primary producers to respond to these inputs. In contrast, at lower elevations, productivity is more likely to be limited by nutrient availability. Although metabolic rates have not been measured extensively in low-elevation lakes, preliminary data suggest metabolic fluxes associated with gross primary production of 1.0 g C·m^{-2}·day^{-1} and ecosystem respiration of 1.3 g C·m^{-2}·day^{-1}, substantially higher rates than found at high-elevation sites. More importantly, the balance between production and respiration shifts in low elevations, and net ecosystem production is negative (–0.3 g C·m^{-2}·day^{-1} in our preliminary data). These flux estimates are supported by landscape patterns in dissolved carbon dioxide concentration that increase with decreasing elevation, and the observation that whereas high-elevation lakes are undersaturated in CO_2 during the growing season, low-elevation lakes remain supersaturated (S. Sadro and J. Sickman, unpublished data), suggesting that terrestrial subsidies are supporting net ecosystem heterotrophy at low elevations.

Changes in bacterial abundance and community composition in Sierra Nevada lakes along landscape gradients in vegetation suggest that terrestrial inputs of DOM subsidize microbial production to a greater extent at low elevations than at high elevations, contributing to larger carbon dioxide fluxes from low-elevation lakes. However, much remains to be learned regarding the magnitude and variation in such fluxes and the extent to which terrestrial carbon is incorporated into higher trophic levels. If carbon is respired without being incorporated into microbial production, or if microbial production simply cycles within the microbial loop without a pathway to higher trophic levels, terrestrial subsidies of DOM may not make their way to higher trophic levels.

In contrast, other forms of terrestrial subsidies may contribute directly to higher order consumers. For example, terrestrial insects can represent a significant portion (29%–38%) of total gut volume in trout in subalpine Castle Lake Vander Zanden et al. 2006). However, terrestrial insect contribution to fish consumers varies by season and the specific type of consumer present in the lake. In Marlette Lake, a small subalpine lake located in the Tahoe Basin, terrestrial insects contribute to rainbow trout (*Oncorhynchus mykiss*) diets with little contribution to the native game fish, Lahontan cutthroat trout (*Oncorhynchus clarkii*; S. Chandra, unpublished data). Despite interannual variability in primary and secondary lake productivity, terrestrial insect contributions seem to be consistent in terms of mass consumed by fish across years, particularly in late summer and fall, when autochthonous sources are less available (S. Chandra, unpublished data). Thus, terrestrial insects may have a stabilizing role in fish energetics and contribute to the maintenance of fish abundances that are higher than what could be supported solely based on autochthonous production. Terrestrial insect in-fall to lakes is likely to be highest at lower elevations, as terrestrial insect biomass decreases with elevation in the Klamath Mountains (K.L. Pope and S.P. Lawler, unpublished data).

Lake-to-land subsidies

Amphibians and aquatic insects represent the most important conduits for the flow of resources from California's mountain lakes to surrounding terrestrial habitats. These organisms have aquatic larvae that metamorphose into terrestrial or semi-terrestrial life stages. Thus, the subsidy takes the form of live animal biomass that emerges from the aquatic habitat.

Amphibians

The amphibian community in California's mountain lakes is represented by four common taxa: ranid frogs (*Rana cascadae*, *Rana muscosa*, and *Rana sierrae*), Pacific chorus frogs (*Pseudacris regilla*), toads (*Anaxyrus boreas* and *Anaxyrus canorus*), and salamanders (*Ambystoma macrodactylum* and *Taricha granulosa*). Ranid frogs and Pacific chorus frogs are the most apparent and abundant amphibians in the majority of California's mountain lakes. The occurrence and abundance of ranid frogs increases with elevation (Knapp 2005; K.L. Pope, unpublished data), whereas the occurrence of Pacific chorus frogs decreases with elevation (Matthews et al. 2001; Knapp 2005). Salamanders are mostly restricted to lakes in the northern Sierra Nevada and Klamath mountains, and the two salamander species tend to occupy different elevation ranges — long-toed salamanders (*A. macrodactylum*) are more likely to be found at higher elevations and rough-skinned newts (*T. granulosa*) are more common at lower elevations (K.L. Pope, unpublished data). Thus, although high-elevation lakes are often dominated by ranid frogs, low-elevation lakes tend to feature a more diverse, but not necessarily more abundant, community of amphibians.

Trout introduction has led to dramatic declines in the abundance of many common amphibian species, especially ranid frogs. Surveys in the Sierra Nevada have shown that lakes with trout are less likely to be occupied by ranid frogs (Knapp and Matthews 2000; Knapp et al. 2003; Knapp 2005) and Pacific chorus frogs (Matthews et al. 2001; Knapp 2005). Similar patterns were observed in the Klamath Mountains, where Cascades frogs (*R. cascadae*), Pacific chorus frogs, and long-toed salamanders were found to be negatively associated with fish (Welsh et al. 2006). The findings of these surveys have been reinforced by fish removal experiments, which have shown that the removal of trout leads to the recovery of ranid frog populations in both the Sierra Nevada (Vredenburg 2004; Knapp et al. 2007) and the Klamath (Pope 2008) mountains. A tadpole caging experiment with Sierra Nevada yellow-legged frogs (*R. sierrae*) confirmed that predation of larvae is an important mechanism for the negative effect of trout on frogs (Vredenburg 2004). Notably, the presence of physical refugia from predation (shallow littoral zones and emergent vegetation) is associated with Cascades frog persistence in lakes occupied

by introduced trout (Hartman et al. 2014). Not all amphibian species are susceptible to predation by trout. There was no relationship between trout and toad occurrence in the Sierra Nevada (Knapp 2005). In the Klamath Mountains, there was no relationship between trout and rough-skinned newt occurrence and even a positive association between trout and boreal toad (*A. boreas*) occurrence. The positive or nonsignificant effects of trout on newts and toads are likely due to the fact that these species secrete potent toxins, which render them unpalatable to trout (Kiesecker et al. 1996; Gunzburger and Travis 2005; Grasso et al. 2010) and other consumers. Overall, trout introduction seems to have a more pronounced effect on amphibian abundance than landscape gradients such as elevation, and the effects of trout on amphibian emergence is likely to be most pronounced at higher elevations, where palatable frogs are the dominant taxa.

In recent decades, an introduced fungal pathogen has emerged as another major factor regulating amphibian abundances. *Batrachochytrium dendrobatidis* (Bd), which causes the disease chytridiomycosis, has led to widespread amphibian declines in the mountains of California. The most notable effects have been on ranid frogs. In the Sierra Nevada, the arrival of Bd has led to the extirpation of mountain yellow-legged frog populations (*R. sierra* and *R. muscosa*) throughout the region (Rachowicz et al. 2006; Vredenburg et al. 2010), resulting in the loss of more than 70% of remaining populations during the past 15 years (R.A. Knapp, unpublished data). While we lack data linking the arrival of Bd to the extirpation of particular populations of Cascades frog (*R. cascadae*), Bd is now present throughout the Californian range of the Cascades frog (Piovia-Scott et al. 2011; Pope et al. 2014). A negative effect of Bd on Cascades frog is indicated by the concordance between the timing of the first appearance of Bd in museum specimens collected from the region and the first-recorded instances of widespread decline in the southern Cascades (M. de Leon, V. Vredenburg, and J. Piovia-Scott, unpublished) and specific outbreaks of Bd that have been associated with dramatic population declines (Piovia-Scott et al. 2015). Bd-related mortality usually occurs shortly after metamorphosis in both mountain yellow-legged frogs (Rachowicz et al. 2006) and Cascades frogs (Hardy et al. 2015). While there is some evidence that Bd infections are more prevalent at higher elevations in the Klamath Mountains (Piovia-Scott et al. 2011), this pattern was not observed in the Sierra Nevada (Knapp et al. 2011). In summary, Bd has led to pronounced declines in amphibian abundance throughout the mountains of California, particularly for the ranid frogs that dominate high-elevation lakes. These declines reduce amphibian emergence from mountain lakes, interrupting lake-to-land subsidies. Even where amphibian populations persist, Bd may reduce the window of availability of juvenile amphibian prey to terrestrial consumers by increasing mortality in recently metamorphosed animals.

Aquatic insects

The abundance and diversity of aquatic insects varies considerably with elevation in California's mountain lakes, with important implications for cross-system resource flows. Here, we focus on insects with aquatic larvae and aerial–terrestrial adult stages, as the emergence of these aerial–terrestrial life stages represents an important flow of resources from lakes to surrounding catchments. The diversity of these biphasic aquatic insects (measured as the number of genera present) and the abundance of the most common orders of these insects (Diptera, Ephemeroptera, Odonata, and Trichoptera) are both reduced in high-elevation lakes (Figs. 1F, 1G), and odonates drop out of the community altogether above ~3000 m in the Sierra Nevada (R.A. Knapp, unpublished data). However, particular taxa that are rare at lower elevation lakes are among the dominant taxa at high-elevation lakes (e.g., *Ameletus* mayflies and *Desmona* caddisflies). While small-bodied Diptera, especially Chironomidae, tend to be the most numerically abundant aquatic insects in California's mountain lakes, the total biomass of emerging aquatic insects is often more closely related to the abundance of larger bodied insects, as they have a higher biomass per individual than chironomids (Finlay and Vredenburg 2007; Pope et al. 2009). Total emerging biomass is higher in littoral zones than in profundal zones (S. Chandra, unpublished data) and peaks in early to mid-summer (K.L. Pope, J. Piovia-Scott, and S.P. Lawler, unpublished data; Epanchin et al. 2010). However, because most of the larger bodied taxa (Ephemeroptera, Trichoptera, Odonata, and Megaloptera) take at least 1 year to complete a generation, their emergence usually occurs in discrete, species-specific pulses (Finlay and Vredenburg 2007; Epanchin et al. 2010) that can occur outside of the early to mid-summer peak emergence period. For example, in subalpine Castle Lake, Odonata tend to emerge between late spring and midsummer, while Ephemeroptera tend to emerge between midsummer and early fall (S. Chandra, unpublished data). Thus, low-elevation lakes are likely to produce a greater biomass of emerging aquatic insects than high-elevation lakes, and this production is likely to be more consistent over the course of the ice-free season. Insect emergence from high-elevation lakes is more likely to consist of a small number of discrete emergence events, during which large portions of the annual insect emergence are transferred to the terrestrial environment during a relatively short period of time.

Introduced trout have pronounced effects on the aquatic stages of biphasic insects, and these effects translate into altered patterns of aquatic insect emergence. The larvae of most large-bodied aquatic insect taxa, including Odonata, Ephemeroptera, and Trichoptera, are negatively affected by trout in both the Sierra Nevada (Knapp et al. 2001*b*, 2005) and the Klamath (Pope et al. 2009; Pope and Hannelly 2013) mountains. This translates into reductions in the biomass of aquatic insects emerging from trout-containing lakes (Finlay and Vredenburg 2007; Pope et al. 2009; Epanchin et al. 2010). Importantly, the effect of trout on insect abundance varies with elevation for some taxa. The large-bodied aquatic insects that inhabit higher elevation lakes seem to be particularly heavily impacted by trout predation (Knapp et al. 2001*b*; R.A. Knapp, unpublished data), perhaps due to the lack of structural refugia (Knapp et al. 2005) or the absence of effective behaviors or camouflage that reduce predation risk (Knapp et al. 2001*b*). In contrast to larger bodied taxa, the effects of introduced trout on smaller bodied Diptera are mixed. In the Sierra Nevada, the total abundance of dipteran larvae tends to be reduced in lakes with trout, an effect that is strongest at lower elevations (R.A. Knapp, unpublished data), and chironomids tended to emerge in greater numbers from lakes in the Klamath Mountains where fish were removed (Pope et al. 2009). However, a study of high-elevation lakes in the southern Sierra Nevada found that mosquitos (*Culex* spp.) are more likely to be present in lakes with trout (Knapp et al. 2001*b*). In summary, trout lead to dramatic reductions in the biomass of emerging aquatic insects, primarily by consuming the larvae of large-bodied species, an effect that is more pronounced in high-elevation lakes.

Amphibian and aquatic insect emergence: flux estimates and spatial patterns

Our estimates confirm that fluxes from lakes to land are generally smaller than those moving from land to lakes. For insect emergence, we estimated a flux of 0.037 g $C \cdot m^{-2} \cdot day^{-1}$ from 16 mid-elevation lakes in the Klamath Mountains, with the bulk of the biomass transfer occurring between mid-July and mid-August; this estimate is based on 3 years of emergence data collected biweekly from 16 mid-elevation lakes in the Klamath Mountains (K.L. Pope, J. Piovia-Scott, and S.P. Lawler, unpublished data). At high-elevation lakes, we expect the total annual flux to be lower and a greater proportion of biomass to emerge during short-duration, species-specific pulses. Amphibian emergence has not been quantified as rigorously as insect emergence at California's mountain lakes, but we have estimated an annual emergence flux on the order of 0.0003 g $C \cdot m^{-2} \cdot day^{-1}$ for Cascades frogs from a lake in the Klamath Mountains with a large population of this species (K.L. Pope, J. Piovia-Scott, and S.P. Lawler, unpublished data); almost all of this emergence took place within a

2- to 3-week window in late summer. These estimates suggest that emerging aquatic insects are likely to represent a greater proportion of the total movement of resources from lakes to catchments than amphibians for most lakes and that emergence is more likely to occur during discrete species-specific pulses at high-elevation lakes.

After emergence, amphibians and aquatic insects are expected to be unevenly distributed in surrounding terrestrial landscapes, with the highest abundances likely to occur near the water (Sabo and Hagen 2012; Bartrons et al. 2013; Muehlbauer et al. 2014; Dreyer et al. 2015). Our data from a set of 16 lakes in the Klamath Mountains confirmed this pattern — aquatic insect biomass was inversely proportional to distance from the lake shore, with a power law best describing the distribution (K.L. Pope, J. Piovia-Scott, and S.P. Lawler, unpublished data). In other words, the biomass of aquatic insects 10 m from the lake shore was approximately twice as high as it was 20 m from the lake shore, and 10 times higher than what would be expected 100 m from shore. Importantly, the biomass of aquatic insects increased with elevation for sampling points close to lakes, suggesting that nearshore habitats at high-elevation lakes may be hotspots for aquatic insect subsidies. While we lack quantitative data on spatial patterns of habitat use by recently metamorphosed amphibians, there are clear life-history differences between taxa that are likely to play an important role in determining the spatial extent of lake-to-land subsidies. For example, the ranid frogs that dominate high-elevation sites are highly aquatic throughout their lives, and postmetamorphic animals tend to remain near lakes and other permanent water sources. In contrast, postmetamorphic chorus frogs, toads, and salamanders spend much more time in temporary wetlands and other more terrestrial habitats and so are likely to be more widely distributed in mountain lake catchments. Interestingly, those species that make extensive use of terrestrial habitats as adults may transport terrestrial resources back to the aquatic habitat when they return to breed (Regester et al. 2006). In summary, the distribution of aquatic insects and amphibians in the terrestrial environment surrounding California's mountain lakes decreases with increasing distance from shore as expected, and although the total amount of biomass transferred may decrease with increasing elevation, spatial patterns of accumulation near the shore are expected to create hotspots for aquatic subsidies even at high-elevation sites.

Effects on terrestrial ecosystems

Amphibians and aquatic insects are an important component of the diet of many terrestrial consumers inhabiting the landscapes surrounding mountain lakes. The distribution and abundance of these consumers are often related to the availability of aquatic prey, a pattern most clearly demonstrated for aerial predators such as birds. In the Sierra Nevada, gray-crowned Rosy Finches (*Leucosticte tephrocotis dawsoni*) are more abundant at lakes without fish, where mayfly (Ephemeroptera) emergence is higher (Epanchin et al. 2010). In the Klamath Mountains, corvids, primarily Clarks Nutcrackers (*Nucifraga columbiana*) and Stellers jays (*Cyanocitta stelleri*), were more abundant at lakes from which fish had been removed than at lakes where fish persisted, and jays have been observed consuming larval Cascades frogs from lakes without fish (K.L. Pope and S.P. Lawler, unpublished data). Other bird species such as Brewers Blackbirds (*Euphagus cyanocephalus*) are also known to feed heavily on frogs in the mountains of California (Bradford 1991). Bats are another common aerial consumer of aquatic resources in California's mountain lake basins, and carbon stable isotope analysis of bats from the Castle Lake catchment suggests that the relative contribution of prey from the aquatic littoral habitat is substantial and varies by season: 100% in late spring, 20% in summer, and 64% in fall (S. Chandra, unpublished data). The reliance on aquatic resources is not limited to winged predators. Garter snake (*Thamnophis* spp.) distributions closely match those of amphibians, a favored prey item, in both the Sierra Nevada (Matthews et al. 2002; Knapp et al. 2005) and the Klamath (Pope et al. 2008) mountains. In addition, postmetamorphic frogs consume emerging aquatic insects, and the frequency of these aquatic prey items in frog diets is reduced at lakes with introduced trout, where the emergence of large-bodied aquatic insects is reduced (Finlay and Vredenburg 2007; Joseph et al. 2011). Although it is likely that terrestrial invertebrates such as spiders and ants also consume aquatic resources, few studies have focused on these taxa. Thus, while there is strong evidence that emerging amphibians and aquatic insects are consumed by a diverse group of terrestrial and aerial consumers and that the presence of fish can negatively impact these consumers by limiting emergence, much remains to be learned with regard to what effect such resource flows have on consumer populations.

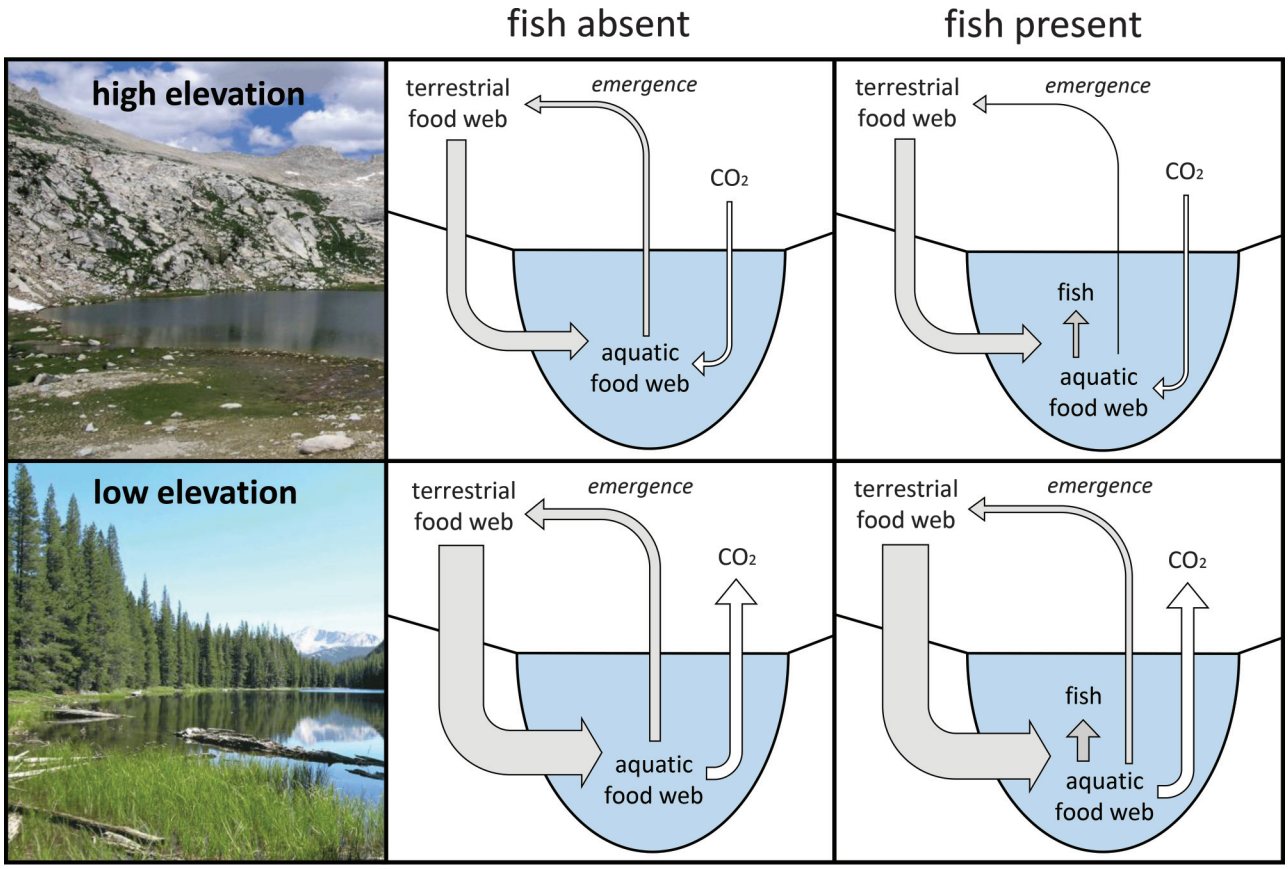
We have little information about how the effects of aquatic resources on terrestrial consumers varies with elevation. While the total flux of resources from the aquatic environment is likely to be reduced at high-elevation lakes, the importance of aquatic resources to terrestrial consumers may actually increase. This is expected to occur because terrestrial insect abundance is also reduced at high elevations, and the ratio of aquatic insects to terrestrial insects can actually increase with elevation in nearshore habitats (K.L. Pope and S.P. Lawler, unpublished data). Given that fish also have more pronounced impacts on emergence at high-elevation lakes, we expect the impact of introduced trout on terrestrial ecosystems to increase with elevation.

A conceptual model of reciprocal linkages in California's mountain lake basins

Here, we present a conceptual model that describes the effects of elevation and introduced trout on reciprocal subsidies between California's mountain lakes and their surrounding terrestrial habitats (Fig. 2). High-elevation lakes sit in catchments dominated by rock, where thin soils and comparatively sparse vegetation limit terrestrial inputs of organic material while increasing inputs of inorganic nitrogen. This leads to an aquatic food web that is largely supported by autotrophic microorganisms and lakes that generally display net autotrophy. For terrestrial and aerial consumers in these high-elevation catchments, emerging insects and amphibians represent a critical prey resource, in part due to the relative paucity of prey resources derived from the low-productivity terrestrial habitat. However, the dominant amphibian and aquatic insect taxa at high-elevation lakes are highly susceptible to predation by introduced trout during their aquatic larval phases, allowing trout to effectively sever the flow of resources out of the lake. Furthermore, the dominant amphibian taxa at high-elevation lakes have been devastated by an introduced pathogen, causing further reductions in the flow of resources out of lakes. Thus, high-elevation terrestrial ecosystems exert few controls on within-lake processes (beyond the passive transport of atmospherically derived nutrients), but within-lake processes exert important controls on terrestrial consumers, as lakes represent a critical source of prey that can be co-opted by introduced predators and pathogens.

In contrast to high-elevation basins, the increased soil development, vegetation, and overall rates of terrestrial productivity found in lower elevation catchments fuel greater terrestrial inputs of organic matter to lakes and limit the availability of inorganic nitrogen. These inputs increase the relative abundance of heterotrophic microorganisms and tilt the lakes towards net heterotrophy. Both autotrophic and heterotrophic production may fuel larval amphibians and insects, leading to the possibility that low-quality terrestrial organic material is recycled to the terrestrial environment in the form of high-quality prey resources. While the flow of aquatic prey resources out of the lake may be less important to terrestrial consumers than at higher elevations due to the high abundance of terrestrially derived resources, asynchrony between the availability of aquatic and terrestrial prey may mean that aquatic prey are a key resource when terrestrial prey are less abundant (primarily at the beginning and end of the snow-free season). The effects of introduced trout on the flow of resources out of the lake are likely to be

Fig. 2. Conceptual model of reciprocal resource subsidies between California's mountain lakes and the surrounding terrestrial habitat. Arrow width is proportional to the relative magnitude of carbon flows; shaded arrows represent organic carbon, open arrows represent inorganic carbon. Carbon flow estimates are described in the text. Low-elevation lakes are expected to have terrestrial carbon inputs that are at least three times greater than those at high-elevation lakes (particulate organic matter fluxes, not included in this estimate, are likely to magnify elevational differences). Differences in the magnitude of terrestrial inputs and within-lake productivity result in high-elevation lakes being sinks for atmospheric carbon dioxide during the ice-free season, while low-elevation lakes emit approximately three times more carbon dioxide than high-elevation lakes fix. Lake-to-land fluxes are estimated to be approximately an order of magnitude lower than land-to-lake fluxes, with relative differences larger at low elevations because of increased terrestrial inputs. Introduced trout may reduce lake-to-land fluxes to virtually zero in high-elevation lakes; this effect is expected to be less severe at low-elevation lakes.



modulated by a combination of decreased susceptibility of amphibian and aquatic insect prey, trophic complexity (e.g., trout remove larger bodied predatory insects, which can have beneficial effects on smaller bodied insects), refuge availability, and increased inputs of insects from the terrestrial environment. Thus, at lower elevations, we expect terrestrial ecosystems to exert important controls on within-lake processes and lakes to represent important hot spots for the remineralization of terrestrial organic materials. However, the role of lakes in supporting terrestrial consumers may be reduced at lower elevations compared with higher elevations.

While many of the patterns and processes synthesized in our conceptual model are well supported by data, a number of key questions remain unanswered. (1) How do introduced trout affect the way that aquatic food webs respond to terrestrial subsidies? (2) How does elevation affect the way that terrestrial food webs respond to aquatic subsidies? (3) How do composition (e.g., insect in-fall vs. detritus, emerging amphibians vs. aquatic insects) and timing (e.g., early season vs. late season) of reciprocal subsidies influence the response in the recipient aquatic or terrestrial ecosystems? Recent advances in the use of deuterium and radiocarbon isotopic tracers, compound-specific isotopic analysis of consumers, and lipid biomarkers are facilitating more detailed studies of the flow of allochthonous and autochthonous material in aquatic and terrestrial food webs. The application of these techniques has the potential to shed light onto some of these unanswered questions.

In summary, we used data from the mountains of California to develop a conceptual model exploring regional variation in reciprocal linkages between lakes and surrounding terrestrial habitats. Our model suggests that the relative importance of subsidies within the landscape shifts along an elevational gradient, with terrestrial subsidies playing a key role in structuring aquatic food webs at lower elevations and aquatic subsidies playing a key role in structuring terrestrial food webs at higher elevations. Introduced aquatic predators and pathogens can disrupt these patterns by limiting the flow of resources out of the aquatic environment, especially at high elevations. This model confirms key results of past studies. For example, we found support for the established ideas that the flux of resources from terrestrial habitats to aquatic habitats is generally greater than the reciprocal flux from water to land (Bartels et al. 2012), that predators on both sides of the aquatic–terrestrial interface often focus on high-quality allochthonous prey resources (Marcarelli et al. 2011; Bartels et al. 2012), and that subsidies are inextricably linked to both food-web and ecosystem processes (Marcarelli et al. 2011). Our model also underscores the notion that lakes play multiple roles in landscapes — in addition to hosting their own complex webs of interactions and energy flows, lakes act both as recyclers of terrestrial organic material and as sources of prey resources for terrestrial consumers (Hanson et al. 2003; Vander Zanden and Gratton 2011; Greig et al. 2012).

In addition to confirming previous findings, our model provides a framework for the empirical exploration of new frontiers in the study of linked ecosystems. By combining a pronounced elevation gradient with a mosaic of predator introductions, we are poised to deepen our understanding of how interactions between top-down and bottom-up forces regulate cross-system exchanges. In addition, the pronounced temporal variation in lake–land subsidy flows allows for an evaluation of how the timing and "pulsedness" (sensu Yang et al. 2008) of reciprocal subsidies generate dynamic feedbacks between aquatic and terrestrial systems (Leroux and Loreau 2011; Richardson and Sato 2015). We hope that this synthesis spurs additional insight into the processes that drive food-web and ecosystem dynamics in complex landscapes.

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References

Bartels, P., Cucherousset, J., Steger, K., Eklöv, P., Tranvik, L.J., and Hillebrand, H. 2012. Reciprocal subsidies between freshwater and terrestrial ecosystems structure consumer resource dynamics. Ecology, **93**(5): 1173–1182. doi:10.1890/11-1210.1. PMID:22764503.

Bartrons, M., Papeş, M., Diebel, M.W., Gratton, C., and Vander Zanden, M.J. 2013. Regional-level inputs of emergent aquatic insects from water to land. Ecosystems, **16**(7): 1353–1363. doi:10.1007/s10021-013-9688-6.

Baxter, C.V., Fausch, K.D., Murakami, M., and Chapman, P.L. 2004. Fish invasion restructures stream and forest food webs by interrupting reciprocal prey subsidies. Ecology, **85**(10): 2656–2663. doi:10.1890/04-138.

Bradford, D.F. 1991. Mass mortality and extinction in a high-elevation population of *Rana muscosa*. J. Herpetol. **25**(2): 174–177. doi:10.2307/1564645.

Brett, M.T., Kainz, M.J., Taipale, S.J., and Seshan, H. 2009. Phytoplankton, not allochthonous carbon, sustains herbivorous zooplankton production. Proc. Natl. Acad. Sci. **106**(50): 21197–21201. doi:10.1073/pnas.0904129106.

Bultman, H., Hoekman, D., Dreyer, J., and Gratton, C. 2014. Terrestrial deposition of aquatic insects increases plant quality for insect herbivores and herbivore density. Ecol. Entomol. **39**(4): 419–426. doi:10.1111/een.12118.

Caraco, N., and Cole, J.J. 2004. When terrestrial organic matter is sent down the river: the importance of allochthonous carbon inputs to the metabolism of lakes and rivers. *In* Food webs at the landscape level. *Edited by* G.A. Polis, M.E. Power, and G.R. Huxel. University of Chicago Press, Chicago, Illinois.

Carlson, R.E. 1977. A trophic state index for lakes1. Limnol. Oceanogr. **22**(2): 361–369. doi:10.4319/lo.1977.22.2.0361.

Carlton, R.G., and Goldman, C.R. 1984. Effects of a massive swarm of ants on ammonium concentrations in a subalpine lake. Hydrobiologia, **111**(2): 113–117. doi:10.1007/BF00008623.

Cole, J.J., Caraco, N.F., Kling, G.W., and Kratz, T.K. 1994. Carbon dioxide supersaturation in the surface waters of lakes. Science, **265**(5178): 1568–1570. doi:10.1126/science.265.5178.1568. PMID:17801536.

Cole, J.J., Carpenter, S.R., Kitchell, J., Pace, M.L., Solomon, C.T., and Weidel, B. 2011. Strong evidence for terrestrial support of zooplankton in small lakes based on stable isotopes of carbon, nitrogen, and hydrogen. Proc. Natl. Acad. Sci. **108**(5): 1975–1980. doi:10.1073/pnas.1012807108.

del Giorgio, P.A., and Peters, R.H. 1994. Patterns in planktonic P:R ratios in lakes: influence of lake trophy and dissolved organic carbon. Limnol. Oceanogr. **39**(4): 772–787. doi:10.4319/lo.1994.39.4.0772.

del Giorgio, P.A.D., Cole, J.J., Caraco, N.F., and Peters, R.H. 1999. Linking planktonic biomass and metabolism to net gas fluxes in northern temperate lakes. Ecology, **80**(4): 1422. doi:10.2307/177085.

Dreyer, J., Townsend, P.A., III, Hoekman, J.C.H., Vander Zanden, D., Gratton, M.J., C. 2015. Quantifying aquatic insect deposition from lake to land. Ecology, **96**(2): 499–509. doi:10.1890/14-0704.1. PMID:26240871.

Epanchin, P.N., Knapp, R.A., and Lawler, S.P. 2010. Nonnative trout impact an alpine-nesting bird by altering aquatic–insect subsidies. Ecology, **91**(8): 2406–2415. doi:10.1890/09-1974.1. PMID:20836462.

Finlay, J.C., and Vredenburg, V.T. 2007. Introduced trout sever trophic connections in watersheds: consequences for a declining amphibian. Ecology, **88**(9): 2187–2198. doi:10.1890/06-0344.1. PMID:17918397.

Francis, T.B., and Schindler, D.E. 2009. Shoreline urbanization reduces terrestrial insect subsidies to fishes in North American lakes. Oikos, **118**(12): 1872–1882. doi:10.1111/j.1600-0706.2009.17723.x.

Francis, T.B., Schindler, D.E., Holtgrieve, G.W., Larson, E.R., Scheuerell, M.D., Semmens, B.X., and Ward, E.J. 2011. Habitat structure determines resource use by zooplankton in temperate lakes: habitat and energetic support of lake zooplankton. Ecol. Lett. **14**(4): 364–372. doi:10.1111/j.1461-0248.2011.01597.x. PMID:21314881.

Gibbons, J.W., Winne, C.T., Scott, D.E., Willson, J.D., Glaudas, X., Andrews, K.M., Todd, B.D., Fedewa, L.A., Wilkinson, L., Tsaliagos, R.N., Harper, S.J., Greene, J.L., Tuberville, T.D., Metts, B.S., Dorcas, M.E., Nestor, J.P., Young, C.A., Akre, T., Reed, R.N., Buhlmann, K.A., Norman, J., Croshaw, D.A., Hagen, C., and Rothermel, B.B. 2006. Remarkable amphibian biomass and abundance in an isolated wetland: implications for wetland conservation. Conserv. Biol. **20**(5): 1457–1465. doi:10.1111/j.1523-1739.2006.00443.x. PMID:17002763.

Goldman, C.R. 1961. The contribution of alder trees (*Alnus tenuifolia*) to the primary productivity of Castle Lake, California. Ecology, **42**(2): 282–288. doi:10.2307/1932080.

Grasso, R.L., Coleman, R.M., and Davidson, C. 2010. Palatability and antipredator response of Yosemite toads (*Anaxyrus canorus*) to nonnative brook trout (*Salvelinus fontinalis*) in the Sierra Nevada Mountains of California. Copeia, **2010**(3): 457–462. doi:10.1643/CH-09-033.

Gratton, C., and Vander Zanden, M.J. 2009. Flux of aquatic insect productivity to land: comparison of lentic and lotic ecosystems. Ecology, **90**(10): 2689–2699. doi:10.1890/08-1546.1. PMID:19886479.

Gratton, C., Donaldson, J., and Vander Zanden, M.J. 2008. Ecosystem linkages between lakes and the surrounding terrestrial landscape in Northeast Iceland. Ecosystems, **11**(5): 764–774. doi:10.1007/s10021-008-9158-8.

Gravel, D., Guichard, F., Loreau, M., and Mouquet, N. 2010. Source and sink dynamics in meta-ecosystems. Ecology, **91**(7): 2172–2184. doi:10.1890/09-0843.1. PMID:20715639.

Greig, H.S., Kratina, P., Thompson, P.L., Palen, W.J., Richardson, J.S., and Shurin, J.B. 2012. Warming, eutrophication, and predator loss amplify subsidies between aquatic and terrestrial ecosystems. Global Change Biol. **18**(2): 504–514. doi:10.1111/j.1365-2486.2011.02540.x.

Gunzburger, M.S., and Travis, J. 2005. Critical literature review of the evidence for unpalatability of amphibian eggs and larvae. J. Herpetol. **39**(4): 547–571. doi:10.1670/1-05A.1.

Hanson, P.C., Bade, D.L., Carpenter, S.R., and Kratz, T.K. 2003. Lake metabolism: relationships with dissolved organic carbon and phosphorus. Limnol. Oceanogr. **48**(3): 1112–1119. doi:10.4319/lo.2003.48.3.1112.

Hardy, B., Pope, K.L., Piovia-Scott, J., Brown, R., and Foley, J. 2015. Itraconazole treatment reduces *Batrachochytrium dendrobatidis* prevalence and increases overwinter field survival in juvenile Cascades frogs. Dis. Aquat. Org. **112**: 243–250. doi:10.3354/dao02813. PMID:25590775.

Hartman, R., Pope, K., and Lawler, S. 2014. Factors mediating co-occurrence of an economically valuable introduced fish and its native frog prey. Conserv. Biol. **28**(3): 763–772. doi:10.1111/cobi.12218. PMID:24372671.

Henschel, J.R., Mahsberg, D., and Stumpf, H. 2001. Allochthonous aquatic insects increase predation and decrease herbivory in river shore food webs. Oikos, **93**(3): 429–438. doi:10.1034/j.1600-0706.2001.930308.x.

Hershey, A.E., Beaty, S., Fortino, K., Keyse, M., Mou, P.P., O'Brien, W.J., Ulseth, A.J., Gettel, G.A., Lienesch, P.W., Luecke, C., Mcdonald, M.E., Mayer, C.H., Miller, M.C., Richards, C., Schuldt, J.A., and Whalen, S.C. 2006. Effect of landscape factors on fish distribution in arctic Alaskan lakes. Freshw. Biol. **51**(1): 39–55. doi:10.1111/j.1365-2427.2005.01474.x.

Hoekman, D., Bartrons, M., and Gratton, C. 2012. Ecosystem linkages revealed by experimental lake-derived isotope signal in heathland food webs. Oecologia, **170**(3): 735–743. doi:10.1007/s00442-012-2329-5. PMID:22526944.

Homyak, P.M., Sickman, J.O., and Melack, J.M. 2014*a*. Pools, transformations, and sources of P in high-elevation soils: implications for nutrient transfer to Sierra Nevada lakes. Geoderma, **217–218**: 65–73. doi:10.1016/j.geoderma.2013.11.003.

Homyak, P.M., Sickman, J.O., and Melack, J.M. 2014*b*. Phosphorus in sediments of high-elevation lakes in the Sierra Nevada (California): implications for internal phosphorus loading. Aquat. Sci. **76**(4): 511–525. doi:10.1007/s00027-014-0350-y.

Hutchinson, G.E. 1970. Eutrophication: past and present. *In* Eutrophication: causes, consequences, correctives. National Academy of Sciences, Washington, D.C. pp. 17–26.

Johnson, D.W., Miller, W.W., Susfalk, R.B., Murphy, J.D., Dahlgren, R.A., and Glass, D.W. 2009. Biogeochemical cycling in forest soils of the eastern Sierra Nevada Mountains, U.S.A. For. Ecol. Manage. **258**(10): 2249–2260. doi:10.1016/j.foreco.2009.01.018.

Joseph, M.B., Piovia-Scott, J., Lawler, S.P., and Pope, K.L. 2011. Indirect effects of introduced trout on Cascades frogs (*Rana cascadae*) via shared aquatic prey. Freshw. Biol. **56**(5): 828–838. doi:10.1111/j.1365-2427.2010.02529.x.

Kiesecker, J.M., Chivers, D.P., and Blaustein, A.R. 1996. The use of chemical cues

in predator recognition by western toad tadpoles. Anim. Behav. **52**(6): 1237–1245. doi:10.1006/anbe.1996.0271.

Knapp, R.A. 2005. Effects of nonnative fish and habitat characteristics on lentic herpetofauna in Yosemite National Park, U.S.A. Biol. Conserv. **121**(2): 265–279. doi:10.1016/j.biocon.2004.05.003.

Knapp, R.A., and Matthews, K.R. 2000. Non-native fish introductions and the decline of the mountain yellow-legged frog from within protected areas. Conserv. Biol. **14**(2): 428–438. doi:10.1046/j.1523-1739.2000.99099.x.

Knapp, R.A., Corn, P.S., and Schindler, D.E. 2001*a*. The introduction of nonnative fish into wilderness lakes: good intentions, conflicting mandates, and unintended consequences. Ecosystems, **4**(4): 275–278. doi:10.1007/s10021-001-0009-0.

Knapp, R.A., Matthews, K.R., and Sarnelle, O. 2001*b*. Resistance and resilience of alpine lake fauna to fish introductions. Ecol. Monogr. **71**(3): 401–421. doi:10.1890/0012-9615(2001)071[0401:RAROAL]2.0.CO;2.

Knapp, R.A., Matthews, K.R., Preisler, H.K., and Jellison, R. 2003. Developing probabilistic models to predict amphibian site occupancy in a patchy landscape. Ecol. Appl. **13**(4): 1069–1082. doi:10.1890/1051-0761(2003)13[1069:DPMTPA]2.0.CO;2.

Knapp, R.A., Hawkins, C.P., Ladau, J., and McClory, J.G. 2005. Fauna of Yosemite National Park lakes has low resistance but high resilience to fish introductions. Ecol. Appl. **15**(3): 835–847. doi:10.1890/04-0619.

Knapp, R.A., Boiano, D.M., and Vredenburg, V.T. 2007. Removal of nonnative fish results in population expansion of a declining amphibian (mountain yellow-legged frog, *Rana muscosa*). Biol. Conserv. **135**(1): 11–20. doi:10.1016/j.biocon.2006.09.013. PMID:17396156.

Knapp, R.A., Briggs, C.J., Smith, T.C., and Maurer, J.R. 2011. Nowhere to hide: impact of a temperature-sensitive amphibian pathogen along an elevation gradient in the temperate zone. Ecosphere, **2**(8): 1–26. doi:10.1890/ES11-00028.1.

Leroux, S.J., and Loreau, M. 2011. Dynamics of reciprocal pulsed subsidies in local and meta-ecosystems. Ecosystems, **15**(1): 48–59. doi:10.1007/s10021-011-9492-0.

Loreau, M., Mouquet, N., and Holt, R.D. 2003. Meta-ecosystems: a theoretical framework for a spatial ecosystem ecology. Ecol. Lett. **6**(8): 673–679. doi:10.1046/j.1461-0248.2003.00483.x.

Marcarelli, A.M., Baxter, C.V., Mineau, M.M., and Hall, R.O. 2011. Quantity and quality: unifying food web and ecosystem perspectives on the role of resource subsidies in freshwaters. Ecology, **92**(6): 1215–1225. doi:10.1890/10-2240.1. PMID:21797150.

Matthews, K.R., Pope, K.L., Preisler, H.K., and Knapp, R.A. 2001. Effects of nonnative trout on Pacific treefrogs (*Hyla regilla*) in the Sierra Nevada. Copeia, **2001**(4): 1130–1137. doi:10.1643/0045-8511(2001)001[1130:EONTOP]2.0.CO;2.

Matthews, K.R., Knapp, R.A., and Pope, K.L. 2002. Garter snake distributions in high-elevation aquatic ecosystems: is there a link with declining amphibian populations and nonnative trout introductions? J. Herpetol. **36**(1): 16–22. doi:10.1670/0022-1511(2002)036[0016:GSDIHE]2.0.CO;2.

McKnight, D.M., Boyer, E.W., Westerhoff, P.K., Doran, P.T., Kulbe, T., and Andersen, D.T. 2001. Spectrofluorometric characterization of dissolved organic matter for indication of precursor organic material and aromaticity. Limnol. Oceanogr. **46**(1): 38–48. doi:10.4319/lo.2001.46.1.0038.

Mehner, T., Attermeyer, K., Brauns, M., Brothers, S., Diekmann, J., Gaedke, U., Grossart, H.-P., Köhler, J., Lischke, B., Meyer, N., Scharnweber, K., Syväranta, J., Vanni, M.J., and Hilt, S. 2015. Weak response of animal allochthony and production to enhanced supply of terrestrial leaf litter in nutrient-rich lakes. Ecosystems, **19**(2): 311–325. doi:10.1007/s10021-015-9933-2.

Miller, W.W., Johnson, D.W., Denton, C., Verburg, P.S.J., Dana, G.L., and Walker, R.F. 2005. Inconspicuous nutrient laden surface runoff from mature forest Sierran watersheds. Water Air Soil Pollut. **163**(1–4): 3–17. doi:10.1007/s11270-005-7473-7.

Muehlbauer, J.D., Collins, S.F., Doyle, M.W., and Tockner, K. 2014. How wide is a stream? Spatial extent of the potential "stream signature" in terrestrial food webs using meta-analysis. Ecology, **95**(1): 44–55. doi:10.1890/12-1628.1.

Murakami, M., and Nakano, S. 2002. Indirect effect of aquatic insect emergence on a terrestrial insect population through by birds predation. Ecol. Lett. **5**(3): 333–337. doi:10.1046/j.1461-0248.2002.00321.x.

Nakano, S., and Murakami, M. 2001. Reciprocal subsidies: dynamic interdependence between terrestrial and aquatic food webs. Proc. Natl. Acad. Sci. **98**(1): 166–170. doi:10.1073/pnas.98.1.166.

Naumann, E. 1919. Nagra synpunkter angaende limnoplanktons okologi med sarskild hansyn till fytoplankton. Sv. Bot. Tidskr. **13**: 129–163.

Nelson, C.E. 2009. Phenology of high-elevation pelagic bacteria: the roles of meteorologic variability, catchment inputs and thermal stratification in structuring communities. ISME J. **3**(1): 13–30. doi:10.1038/ismej.2008.81. PMID:18784755.

Nelson, C.E., Sadro, S., and Melack, J.M. 2009. Contrasting the influences of stream inputs and landscape position on bacterioplankton community structure and dissolved organic matter composition in high-elevation lake chains. Limnol. Oceanogr. **54**(4): 1292–1305. doi:10.4319/lo.2009.54.4.1292.

Odum, E.P. 1969. The strategy of ecosystem development. Science, **164**(3877): 262–270. doi:10.1126/science.164.3877.262. PMID:5776636.

Pace, M.L., Cole, J.J., Carpenter, S.R., Kitchell, J.F., Hodgson, J.R., Van de Bogert, M.C., Bade, D.L., Kritzberg, E.S., and Bastviken, D. 2004. Whole-lake carbon-13 additions reveal terrestrial support of aquatic food webs. Nature, **427**(6971): 240–243. doi:10.1038/nature02227. PMID:14724637.

Piovia-Scott, J., Pope, K.L., Lawler, S.P., Cole, E.M., and Foley, J.E. 2011. Factors related to the distribution and prevalence of the fungal pathogen *Batrachochytrium dendrobatidis* in *Rana cascadae* and other amphibians in the Klamath Mountains. Biol. Conserv. **144**(12): 2913–2921. doi:10.1016/j.biocon.2011.08.008.

Piovia-Scott, J., Pope, K., Worth, S.J., Rosenblum, E.B., Poorten, T., Refsnider, J., Rollins-Smith, L.A., Reinert, L.K., Wells, H.L., Rejmanek, D., Lawler, S., and Foley, J. 2015. Correlates of virulence in a frog-killing fungal pathogen: evidence from a California amphibian decline. ISME J. **9**(7): 1570–1578. doi:10.1038/ismej.2014.241. PMID:25514536.

Polis, G.A., Anderson, W.B., and Holt, R.D. 1997. Toward an integration of landscape and food web ecology: the dynamics of spatially subsidized food webs. Annu. Rev. Ecol. Syst. **28**: 289–316. doi:10.1146/annurev.ecolsys.28.1.289.

Polis, G.A., Power, M.E., and Huxel, G.R. 2004. Food webs at the landscape level. University of Chicago Press, Chicago, Illinois.

Pope, K.L. 2008. Assessing changes in amphibian population dynamics following experimental manipulations of introduced fish. Conserv. Biol. **22**(6): 1572–1581. doi:10.1111/j.1523-1739.2008.00998.x. PMID:18680499.

Pope, K.L., Garwood, J.M., Welsh, H.H., and Lawler, S.P. 2008. Evidence of indirect impacts of introduced trout on native amphibians via facilitation of a shared predator. Biol. Cons. **141**(6): 1321–1331. doi:10.1016/j.biocon.2008.03.008.

Pope, K.L., and Hannelly, E.C. 2013. Response of benthic macroinvertebrates to whole-lake, non-native fish treatments in mid-elevation lakes of the Trinity Alps, California. Hydrobiologia, **714**(1): 201–215. doi:10.1007/s10750-013-1537-2.

Pope, K.L., Piovia-Scott, J., and Lawler, S.P. 2009. Changes in aquatic insect emergence in response to whole-lake experimental manipulations of introduced trout. Freshw. Biol. **54**(5): 982–993. doi:10.1111/j.1365-2427.2008.02145.x.

Pope, K.L., Brown, C., Hayes, M., Green, G., and Macfarlane, D. 2014. Cascades frog conservation assessment. USDA Forest Service, Pacific Southwest Research Station, General Technical Report PSW-GTR-244.

Prairie, Y.T., Bird, D.F., and Cole, J.J. 2002. The summer metabolic balance in the epilimnion of southeastern Quebec lakes. Limnol. Oceanogr. **47**(1): 316–321. doi:10.4319/lo.2002.47.1.0316.

Rachowicz, L.J., Knapp, R.A., Morgan, J.A.T., Stice, M.J., Vredenburg, V.T., Parker, J.M., and Briggs, C.J. 2006. Emerging infectious disease as a proximate cause of amphibian mass mortality. Ecology, **87**(7): 1671–1683. doi:10.1890/0012-9658(2006)87[1671:EIDAAP]2.0.CO;2. PMID:16922318.

Regester, K.J., Lips, K.R., and Whiles, M.R. 2006. Energy flow and subsidies associated with the complex life cycle of ambystomatid salamanders in ponds and adjacent forest in southern Illinois. Oecologia, **147**(2): 303–314. doi:10.1007/s00442-005-0266-2. PMID:16200399.

Richardson, J.S., and Sato, T. 2015. Resource subsidy flows across freshwater–terrestrial boundaries and influence on processes linking adjacent ecosystems. Ecohydrology, **8**(3): 406–415. doi:10.1002/eco.1488.

Sabo, J.L., and Hagen, E.M. 2012. A network theory for resource exchange between rivers and their watersheds. Water Resour. Res. **48**(4): W04515. doi:10.1029/2011WR010703.

Sabo, J.L., and Power, M.E. 2002. River–watershed exchange: effects of riverine subsidies on riparian lizards and their terrestrial prey. Ecology, **83**(7): 1860–1869. doi:10.1890/0012-9658(2002)083[1860:RWEEOR]2.0.CO;2.

Sadro, S., and Melack, J.M. 2012. The effect of an extreme rain event on the biogeochemistry and ecosystem metabolism of an oligotrophic high-elevation lake. Arctic Antarctic Alpine Res. **44**(2): 222–231. doi:10.1657/1938-4246-44.2.222.

Sadro, S., Melack, J.M., and MacIntyre, S. 2011*a*. Depth-integrated estimates of ecosystem metabolism in a high-elevation lake (Emerald Lake, Sierra Nevada, California). Limnol. Oceanogr. **56**(5): 1764–1780. doi:10.4319/lo.2011.56.5.1764.

Sadro, S., Melack, J.M., and MacIntyre, S. 2011*b*. Spatial and temporal variability in the ecosystem metabolism of a high-elevation lake: integrating benthic and pelagic habitats. Ecosystems, **14**(7): 1123–1140. doi:10.1007/s10021-011-9471-5.

Sadro, S., Nelson, C.E., and Melack, J.M. 2011*c*. Linking diel patterns in community respiration to bacterioplankton in an oligotrophic high-elevation lake. Limnol. Oceanogr. **56**(2): 540–550. doi:10.4319/lo.2011.56.2.0540.

Sadro, S., Nelson, C.E., and Melack, J.M. 2012. The influence of landscape position and catchment characteristics on aquatic biogeochemistry in high-elevation lake-chains. Ecosystems, **15**(3): 363–386. doi:10.1007/s10021-011-9515-x.

Scharnweber, K., Vanni, M.J., Hilt, S., Syväranta, J., and Mehner, T. 2014. Boomerang ecosystem fluxes: organic carbon inputs from land to lakes are returned to terrestrial food webs via aquatic insects. Oikos, **123**(12): 1439–1448. doi:10.1111/oik.01524.

Schriever, T.A., Cadotte, M.W., and Williams, D.D. 2013. How hydroperiod and species richness affect the balance of resource flows across aquatic–terrestrial habitats. Aquat. Sci. **76**(1): 131–143. doi:10.1007/s00027-013-0320-9.

Sickman, J.O., Leydecker, A., and Melack, J.M. 2001. Nitrogen mass balances and abiotic controls on N retention and yield in high-elevation catchments of the Sierra Nevada, California, United States. Water Resour. Res. **37**(5): 1445–1461. doi:10.1029/2000WR900371.

Sickman, J.O., Leydecker, A.L., Chang, C.C., Kendall, C., Melack, J.M., Lucero, D.M., and Schimel, J. 2003*a*. Mechanisms underlying export of N from high-

elevation catchments during seasonal transitions. Biogeochemistry, **64**(1): 1–24. doi:10.1023/A:1024928317057.

Sickman, J.O., Melack, J.M., and Clow, D.W. 2003*b*. Evidence for nutrient enrichment of high-elevation lakes in the Sierra Nevada, California. Limnol. Oceanogr. **48**(5): 1885–1892. doi:10.4319/lo.2003.48.5.1885.

Solomon, C.T., Carpenter, S.R., Clayton, M.K., Cole, J.J., Coloso, J.J., Pace, M.L., Vander Zanden, M.J., and Weidel, B.C. 2011. Terrestrial, benthic, and pelagic resource use in lakes: results from a three-isotope Bayesian mixing model. Ecology, **92**(5): 1115–1125. doi:10.1890/10-1185.1. PMID:21661572.

Vander Zanden, M.J., and Gratton, C. 2011. Blowin' in the wind: reciprocal airborne carbon fluxes between lakes and land. Can. J. Fish. Aquat. Sci. **68**(1): 170–182. doi:10.1139/F10-157.

Vander Zanden, M.J., Chandra, S., Park, S.-K., Vadeboncoeur, Y., and Goldman, C.R. 2006. Efficiencies of benthic and pelagic trophic pathways in a subalpine lake. Can. J. Fish. Aquat. Sci. **63**(12): 2608–2620. doi:10.1139/f06-148.

Vicars, W.C., Sickman, J.O., and Ziemann, P.J. 2010. Atmospheric phosphorus deposition at a montane site: size distribution, effects of wildfire, and ecological implications. Atmos. Environ. **44**(24): 2813–2821. doi:10.1016/j.atmosenv.2010.04.055.

Vredenburg, V.T. 2004. Reversing introduced species effects: experimental removal of introduced fish leads to rapid recovery of a declining frog. Proc. Natl. Acad. Sci. U.S.A. **101**(20): 7646–7650. doi:10.1073/pnas.0402321101. PMID:15136741.

Vredenburg, V.T., Knapp, R.A., Tunstall, T.S., and Briggs, C.J. 2010. Dynamics of an emerging disease drive large-scale amphibian population extinctions. Proc. Natl. Acad. Sci. U.S.A. **107**(21): 9689–9694. doi:10.1073/pnas.0914111107. PMID:20457913.

Welsh, H.H., Pope, K.L., and Boiano, D. 2006. Sub-alpine amphibian distributions related to species palatability to non-native salmonids in the Klamath Mountains of northern California. Divers. Distrib. **12**(3): 298–309. doi:10.1111/j.1366-9516.2006.00254.x.

Williams, M.W., and Melack, J.M. 1991. Precipitation chemistry in and ionic loading to an alpine basin, Sierra Nevada. Water Resour. Res. **27**(7): 1563–1574. doi:10.1029/90WR02773.

Williamson, C.E., Morris, D.P., Pace, M.L., and Olson, O.G. 1999. Dissolved organic carbon and nutrients as regulators of lake ecosystems: resurrection of a more integrated paradigm. Limnol. Oceanogr. **44**(3 part 2): 795–803. doi:10.4319/lo.1999.44.3_part_2.0795.

Yang, L.H., Bastow, J.L., Spence, K.O., and Wright, A.N. 2008. What can we learn from resource pulses. Ecology, **89**(3): 621–634. doi:10.1890/07-0175.1. PMID:18459327.