The Resilience of the Rumen Microbial Population

Paul J. Weimer[1]
Department of Bacteriology
University of Wisconsin-Madison

Abstract

In healthy dairy cows, rumen microbial community composition is highly individualized by host animal; displays modest inertia when host diet is altered; and displays impressive resilience when perturbations are relaxed. The mechanisms underlying this resilience are poorly understood, but appear to involve intrinsic properties of the microbial community that work in concert with metabolic, immunological, and behavioral contributions from the host. Attempts to modify the ruminal community by strain inoculation or whole-community exchange generally achieve only transient shifts in community composition. By contrast, dysbiotic cows appear to be more amenable to manipulation of their communities to restore their function, suggesting a natural tendency of the rumen to achieve a stable functional community. While microbial community composition appears to affect performance metrics, such as milk production efficiency and milk composition, manipulating the communities to improve overall performance remains elusive, although analysis of community composition may provide a tool to inform management strategies and culling decisions. Owing to the difficulty of manipulating rumen microbial community composition in adult animals, there has been much interest in early-life (pre-weaning) interventions to direct the development of the community prior to maturity.

Introduction

The ruminant animal is defined by the presence of a specific gastrointestinal organ, the rumen, in which a complex and highly adapted microbial community carries out an anaerobic conversion of feed materials to VFA and microbial cell mass that respectively provide the main energy and protein sources to nourish the host animal. Establishment and evolution of this complex community occurs gradually as the organ itself develops within a juvenile, originally monogastric host. Once established, this community drives the ability of the host to utilize a wide variety of feed components, including fibrous plant materials that cannot be significantly digested by non-ruminants. Owing to these spectacular and irreversible benefits exchanged between the animal and its microbiome, the ruminant is unsurpassed as an example of host/microbe mutualism.

From a microbial ecology standpoint, the rumen can be considered as its own ecosystem, in which fairly stable environmental conditions (temperature, pressure, and water content) interact with additional variables – particularly the chemical composition of inputs (diet) and the rate of passage of materials – to set the conditions that regulate the microbial metabolic processes. Early studies in rumen microbiology were facilitated by Hungate's development of anaerobic culture methods, which permitted

---

[1] Contact at: Microbial Sciences Center, 1550 Linden Drive, Madison, WI 53706, (608) 770-6071, Email: pjweimer@wisc.edu.

isolation and characterization of a limited number of individual microbial species. These species could readily be isolated from almost all ruminants tested. And because, taken together, they appeared to encompass most of the substrate conversions known to occur in the rumen, it was long thought that the ruminal community was similar across all individual ruminants within a species, and even across multiple species within the ruminant order.

The development in the 1990s of more sophisticated, culture-independent methods for characterizing microbial communities revealed that all microbial communities in nature, including those of the rumen, were far more complex and diverse than were indicated by culture-dependent methods. We now know that, although the rumen contains a "core microbiome" (i.e., a collection of species that are present in most individual ruminants), there are a large number of other species present as well (Jami and Mizrahi, 2012; Henderson et al., 2015). Moreover, the abundance of individual microbial species – both core and non-core -- varies considerably both within and across individuals over time. Although much of the variation in community composition is driven by diet (some examples of which will be given below), there are substantial differences in community composition among animals fed the same diet. This has led to the concept of host-specificity, i.e., microbiomes individualized to their specific host. This concept has recently been noted, with great fanfare, in the human gastro intestinal (**GI**) tract (Lozupone et al., 2012; Lynch and Pederson, 2015), but interestingly was first demonstrated in the rumen way back in the 1930s for protozoa (Kofoid and MacLennan, 1933), and in the 1990s for bacteria (Weimer, 1998), and only recently for methanogens (Zhou et al., 2012).

Central to the concept of host individuality is the notion that the microbial community is relatively stable when environmental conditions and inputs (e.g., feed composition) are stable, and displays some resistance to change when conditions are changed. In other words, the community would display the ecological property of *inertia* (Table 1; sometimes termed *resistance* [Allison and Martiny, 2008]). The inertia of the community would allow its composition to be maintained within a reasonable range, even as the community undergoes some changes in its composition over time (i.e., during a feeding cycle, or across months). Moreover, host individuality would also imply that the community, once perturbed (for example, by a substantial change in diet), would be able to re-stabilize itself once the perturbation was removed. In other words, the community would display the ecological property of *resilience* (Table 1). We can employ a simple metaphor to characterize these properties: If the microbial community can be regarded as a rubber band, inertia describes the deformation of the band. How far can it be stretched, and how far does it stretch for a particular input of effort? By contrast, resilience describes the relaxation of the band. Once the stress is removed, does the band return to its original conformation (i.e., display *elasticity* [Table 1]), and how rapidly does the return occur? We will consider these two properties in turn.

Relevant Properties of Microbial Communities

Inertia

Diet appears to be the major force that overcomes the natural inertia of the rumen microbial community (Henderson et al., 2015). Numerous studies have shown that, within individual animals, changing the diet results in changes in prokaryotic (bacterial and archaeal) communities; changes are much less detectable in the protozoal communities (deMenezes et al., 2011). In fact, diet-induced changes in prokaryotic community composition appear to be much stronger, and occur much more rapidly, in ruminants than in humans, whose bacterial communities generally fall into one of three “enterotypes”, within which diet-induced differences are “small compared to baseline interpersonal variations” (Lozupone et al., 2012).

In ruminants, changes in microbial community composition might be expected during the course of the feeding cycle, owing to the different rates of utilization of different feed components, which would lead to time-dependent changes in the composition of the remaining, undegraded feed. In fact, bacterial community composition (**BCC**) was shown to change both within and across feeding cycles in cows fed the same TMR at 12 h intervals (Welkie et al., 2010). Interestingly, BCC returned to a different end-point at the end of each of 4 successive feeding cycles, suggesting that BCC is actually in a continual state of flux (i.e., is not completely elastic). Nevertheless, several studies with cows fed once-daily have shown that BCC measured in individual cows at the same time after feeding over the last 3 days of a 28-day experimental period showed much greater similarity to one another than to the BCC of other cows on the same diet and that displayed similar production metrics.

One interesting aspect of dietary effects is that even a modest change in diet can have a major effect on specific taxa. For example, Mohammed et al. (2014) used automated ribososomal intergenic spacer analysis (**ARISA**) and next-generation sequencing (**NGS**) to characterize the bacterial community in heifers that were either grazed fresh orchardgrass pasture (**OP**) for 3 consecutive 28-day periods, or were alternated from OP to orchardgrass hay (**OH**) and then returned to OP over successive 28-day periods. Heifers whose diets were switched to OH showed significant decreases in the relative population size of genus *Butyrivibrio* (one of the most abundant genera in the rumen) along with a decrease in the molar proportion of ruminal butyrate and an increase in the molar proportion of ruminal acetate. Such changes may have resulted from OH’s lower level of water-soluble carbohydrates, a preferred substrate for *Butyrivibrio*. Both the molar proportion of butyrate and the relative abundance of *Butyrivibrio* returned to their previous levels when the heifers were returned to OP, providing an indication of the elasticity of this particular genus within the rumen bacterial community.

One of the more interesting principles that has emerged from theoretical studies in microbial ecology relates to the effects of positive and negative interactions among community members on community stability. Surprisingly, while cooperative interactions among species can improve overall efficiency of the community, they tend to destabilize rather than stabilize communities (Coyte et al., 2015). Consequently, interspecific competition actually makes the community more stable, i.e., display greater inertia, and the effects of this competition become more important as community diversity increases. This conclusion is a bit counterintuitive, as it goes against our general notion that one of the hallmarks of the ruminal community is its complex network of cooperative interactions (such as interspecies hydrogen transfer and cross-feeding of nutrients among different metabolic classes of microbes). However, when one considers the large number of closely-related species within the rumen, which presumably have substantial overlap of function, it is likely that competition for substrate is intense, whether it be for colonizable surfaces of feed particles, or soluble substrates present at concentrations similar to those of the transport coefficients of microbes that use these substrates.

What forces, then, drive resilience of the ruminal community? In the case of a dietary shift followed by return to the original diet, competition is likely a major driver. If competition was the dominant interaction on the original diet, new competitive interactions would result from a change in the availability of a new group of substrates, and a return to the original diet should again favor the original competitions that led to the establishment of the original community.

Resilience

The resilience of the rumen microbial community is further (and more dramatically) demonstrated by ruminal contents exchange experiments. Near-total (~95%) exchange of ruminal contents between multiparous ruminally cannulated Holstein cows resulted in gradual return, over the course of several weeks, to a community composition similar to that in the recipient host, even though the donor inoculum was derived from a cow fed the adjacent diet and subjected to the same environmental conditions (i.e., housed in an adjacent tie stall; Weimer et al., 2010a; Weimer et al., 2017). Perhaps more surprising is the observation that differences in ruminal chemistry between donor and recipient cows were overcome in the recipient within a day of the contents exchange, suggesting that the cow has substantial control over her own ruminal chemistry, whether it be by controlling the rate of VFA absorption, rate of passage, or the volume and composition of salivary buffers. In some exchange experiments, the differences in ruminal chemistry may strongly influence microbial community composition, and thus partially explain community resilience. However, community resilience has also been demonstrated in exchange experiments between cows that had similar ruminal chemistries (Weimer et al., 2017).

While resilience has been demonstrated experimentally, the underlying mechanisms have received little study. Presumably resilience is determined by the strengths of the interactions (positive and negative) among the different community members, and the degree to which the individual animal has strengthened its mutualism with its own community. While we may speculate on these various determinants of resilience (Table 2), at present we have little knowledge as to their relative contribution.

One would expect that in these exchange experiments, the donor community would also be highly competitive (because it had developed on the same diet, albeit in another host). But this new community is eventually displaced by the recipient's original community, which suggests that the primary determinant of community composition is the interactions between the host and her individualized host community. The likely complexity of these interactions may explain why a return to the original community composition following contents exchange is slower than the shift in community composition following dietary change without further addition of exogenous microbes.

Impacts of Host Individuality and Resilience on Dairy Production Traits

Where does resilience fit into the general concepts of how microbial communities behave? In what way does resilience of the community affect how we should be feeding cows? And how does it affect our ability to manipulate the ruminal community to improve animal performance?

The resilience of the rumen community appears to substantially exceed that of most other microbial habitats. Soil communities appear to recover only slowly from perturbation (Allison and Martiny, 2008) and anaerobic digesters are often subject to failure upon drastic changes in the type and rate of substrate loading (Chen et al., 2008). The ruminal community does not experience such failures, and as a result, our focus can shift to a more practical issue -- how community composition might affect, or even improve, animal performance. Resilience remains an important aspect of this relationship because conditions that perturb the community may affect performance, and recovery of performance may require re-establishment of the pre-disturbance community.

Feed efficiency

In beef cattle production, measurement of feed efficiency in the feedlot is relatively simple, owing to the continuous increase in weight over the grow-out period. Feed efficiency can be expressed as average daily gain per unit of DM intake. This can be a bit misleading because it does not necessarily reflect the variation in metabolic efficiency of different animals due to the effect of maintenance requirements, which varies with BW. An alternative way of expressing feed efficiency is residual feed intake (**RFI**), which is the difference between the amount of feed required to produce one unit of output in an individual animal versus that predicted from regression data obtained from a cohort of animals of the same age, fed the same diet, and housed under the same conditions (Koch et al., 1963). By this measure, steers with a positive RFI require more feed to produce the same weight gain (i.e., are less efficient), while those with a negative RFI require less feed to produce the same weight gain (i.e., are more efficient). The advantage of RFI is that it allows direct comparison of animals at the same level of production. Five major physiological processes have been suggested to account for the variation in RFI among steers, 2 of which (digestibility and heat increment plus fermentation) have been suggested to account in aggregate for about 19% of the variation (Herd and Arthur, 2009).

In dairy cows, feed efficiency is more complicated because the output variable (energy corrected milk, **ECM**) is affected by the metabolic demands of pregnancy and by changes in body composition, particularly in the periparturient period. As a result, RFI changes continuously over the lactation cycle. Thus, when comparing feed efficiency among cows, it is important to obtain measurements at the same stage of lactation, preferably within the same range of days in milk (**DIM**). In contrast to beef cattle, there are no studies that have explicitly partitioned the relative contribution of different physiological processes to feed efficiency in dairy cows.

A key measure of feed efficiency in dairy cows, namely milk production efficiency (**MPE**, expressed as ECM/DMI) varies substantially among animals on the same diet at the same stage of lactation. RFI, which can also be used as a surrogate for feed efficiency in cows, is considered to be moderately heritable, although heritability (h^2) values have varied widely among studies (Connor, 2015). However, within cohorts of cows under the same management conditions, a substantial portion of the variation in RFI is not explained by genetics. Is some of this variation explained by inter-animal differences in their ruminal microbiomes? Two studies (Jami et al., 2014; Jewell et al., 2015) have shown that groups of cows divergent in MPE (as assessed by RFI) have different microbial communities. Substantial differences have been noted in the relative abundance of individual bacterial species ("operational taxonomic units", or **OTU**, in microbial ecology parlance) between high- and low-efficiency cows. Shabat et al. (2016) have further shown that the rumen fluid of cows of higher MPE contain a higher molar proportion of propionate, and elevated levels of 2 specific species, *Megasphaera elsdenii* and *Coprococcus catus* (assessed by not only conventional 16S rRNA sequencing, but also a metagenomics analysis). However, both taxa represented only a tiny fraction of the bacterial community (<0.01%), casting some doubt on how they could have an outsized effect on the performance of the whole community. Further research aimed at establishing the potential relationships are clearly warranted.

In order to determine if microbial communities directly determine differences in MPE (rather than merely being associated with differences in MPE), we performed near-total exchange of ruminal contents between pairs of ruminally cannulated cows [using 3 pairs identified in the Jewell et al. (2015) study] that differed in DMI at the same level of ECM (Weimer et al., 2017). Detecting patterns of change in MPE following exchange was complicated by the general difficulty of accurately measuring MPE over short time periods, and by the fact that the cows were in different stages of lactation at the time of the contents exchange. Nevertheless, we did observe short-term trends in MPE following the exchange. For all 3 of the low-efficiency (**LE**) cows, MPE increased upon receipt of the ruminal contents of the high efficiency (**HE**) cows, and for 2 of the 3 HE cows, MPE decreased to a greater extent following receipt of the contents from the LE cows. Surprisingly, the other HE cow displayed an increase in MPE following receipt of the contents from her LE pair-mate. The effects on MPE were transient, however: by day 10 post- exchange, all the cows displayed MPE consistent with that expected had the exchange not taken place. Examination of BCC using next-generation sequencing revealed that the BCC resembled that of the donor cow at the time of the exchange, but within ~10 days had returned toward that of the donor cow. This provides a further confirmation of community resilience, as well as more direct evidence of a microbial influence on MPE. However, it also points out that some cows may not have fully optimized their community composition, which may be amenable to manipulation.

The rumen microbial community has a high degree of species diversity, and as noted above, there is evidence from modeling studies that diversity has an unexpected destabilizing effect on the community. Diversity also seems have a relationship with milk production efficiency. Both Shabat et al. (2016) and Weimer et al. (2017) have observed that species diversity is lower in cows that have a higher milk production efficiency. It can be argued that the high-efficiency communities are more “refined”, i.e., are less encumbered by low-abundance species that do not effectively contribute to the metabolic or energetic efficiency of the ruminal fermentation.

Milk composition

Milk composition, particularly the percentages of fat, protein and lactose, are major determinants of not only milk’s nutritional value, but also the price paid to producers. In most of the US, fat is the most valuable component. Fat levels below 3.2% in Holstein cows provide a common definition of milk fat depression (**MFD**), a costly condition that is often induced by certain dietary combinations. The primary mechanism for MFD is the ruminal accumulation, and translocation to the mammary gland, of certain unsaturated fatty acids, particularly *trans*-10, *cis*-12 linoleic acid, a potent repressor of mik fat synthesis. Because ruminal microbes are known to participate in isomerization and biohydrogenation of these long-chain unsaturated acids, their involvement in MFD has long been suspected, but the role of specific taxa has remained elusive.

One intriguing aspect of MFD is that the fat test response to a given diet varies markedly among individual cows (Weimer et al., 2010b). When switched across TMR that contained corn oil but varied in the rate of starch fermentability and the presence of monensin, some cows showed no change in milk fat levels. Others showed MFD immediately upon substitution by the rapidly fermenting starch, while others displayed MFD only when the diet was further altered by inclusion of monensin. Moreover, after withdrawal of the monensin, some cows regained milk fat, while others remained fat depressed for several months. Examination of the bacterial communities using ARISA revealed shifts in BCC that were consistent with the fat test response: non-responding cows showed only slight shifts in BCC. Cows whose MFD was reversible showed a partial return of BCC to the pre-MFD community, while cows whose fat test remained low had BCC that were far removed from those of the original, pre-MFD BCC. Overall, the results indicate that cows vary in their resilience, or at least in the rate at which they recovered their milk fat production, and the rate at which their bacterial community ultimately returns the composition of the original, pre-disturbed community.

Recovery from diet-induced MFD has been investigated in more detail by Rico et al. (2014; 2015). Inoculation of MFD cows with ruminal contents from non-MFD cows did not improve overall fat yield, but did slightly accelerate recovery of de novo FA synthesis and normal ruminal FA biohydrogenation (Rico et al., 2014). In addition, recovery was accompanied by rapid changes (over a few days) in the relative abundance of particular taxa, in most cases to resemble their abundances prior to MFD induction (Rico et al., 2015).

What About Sick Cows?

Up to now, we have noted and documented the resilience of the ruminal community in healthy adult cows fed conventional diets. What about "dysbiotic" cows whose ruminal community has been compromised by illness (for example, metabolic disorders or a nutritional toxicosis) to the point that its function has been impaired? Can such cows restore their ruminal community composition on their own, or can producers or veterinarians assist in the restorative process?

In fact, the process of "transfaunation" (i.e., direct ruminal contents transfer from a healthy donor cow to a dysbiotic recipient) is widely practiced, and this topic has been recently reviewed (De Peters and George, 2014). Transfer of 8 to 16 L of rumen fluid from healthy cows on diets similar to that of the recipient sick animal has been recommended, although success may also hinge on prior partial removal, via stomach tube, of as much dysbiotic digesta as possible. This practice finds analogy to the currently faddish fecal microbiota transplants carried out to correct chronic intestinal dysbiosis in human subjects (Grehan et al., 2010). As pointed out by De Peters and George (2014), practical development of transfaunation methods in ruminants has outpaced our understanding of the mechanisms underlying its success. Clearly, transfaunation provides mechanical stimulation to a static (atonic) rumen, along with VFA and other nutrients to the dysbiotic host (which typically has gone off of feed and is thus likely to be metabolically stressed). Nevertheless, we can speculate on the nature of the transfaunation process from the standpoint of microbial ecology: the dysbiotic state is likely maintained by an unstable collection of ruminal microbes that interact ineffectively, resulting in poor metabolism of (and energy harvest from) feeds, and in ancillary disruptions in host-microbe interactions (e.g., interkingdom signaling). This community can be supplanted, via transfaunation, by a more highly functional community whose members interact more effectively with each other (either by competition or cooperation) and with the host, and which may obtain a higher yield of energy (and thus faster and more complete microbial growth), with an eventual re-stabilization of host-microbe interactions.

Applying the Lessons of Host Individuality and Community Resilience to Ruminant Production

Implications for animal science research

The resilience of the ruminal community provides a lens through which both producers and consumers of animal science research can formulate and interpret animal feeding studies. Historically, feeding studies have been conducted with a view that adaptation of the rumen microbial community occurs by the time production and microbiological data are collected near the end of each time period within an experiment -- typically 14 to 8 days – but the time periods selected have been based more on personal preference than on systematic analysis. We have observed that BCC stabilizes within the last few days of 28-day periods when dietary changes across period were modest (Weimer et al., 2010b). More recent studies (Machado et al., 2016) have revealed that in beef steers subjected to a switch from sugarcane to corn silage, adaptation of BCC at the phylum level, at least in the liquid phase of ruminal contents, was quite rapid (mean = 7.2 days, range = 3 to 9 days). Although finer-scale taxonomic measurements were not made in that study, it appears that the adaptation period of the community may generally be more rapid than previously suspected. Shorter experimental periods can greatly reduce the overall costs of dairy trails and would allow experiments to be conducted over a narrower time range, thereby minimizing effects of stage of lactation.

A second consideration involves the common use of Latin squares for nutritional studies. Such designs are prized for their compactness (low animal numbers) and their statistical power, but they may not be appropriate for all studies. If a subset of cows within a study have microbial communities that display particularly strong inertia or poor resiliency, they could skew the results because their communities have not stablilized by the time the next dietary treatment is appliled.

Modifying or redirecting microbial community composition

The potential of altering microbial community function through manipulation of its composition has long fascinated both animal scientists and rumen microbiologists. Several successes have been achieved in establishing inoculated strains (usually by direct dosing) to overcome nutritional toxicoses, such as poisoning by mimosine (Jones and Megarrity, 1986) or fluoroacetate (Gregg et al., 1998). By contrast, numerous attempts to improve fiber digestion or to decrease losses of feed to methane or ammonia, via inoculation of bacterial monocultures, have almost always resulted in failure, going all the way back the seminal work of Varel et al. (1995). Success appears to require the availability of an open niche that the inoculated strain can fill (Weimer, 1998). Ruminal contents exchange experiments (detailed above) have also resulted in only transient shifts in microbial community composition, apparently due to the lack of selective pressure to overcome a well-established indigenous community in mature host animals. This has led to proposals that early interventions (i.e., inoculating calves prior to weaning, or even at birth) may provide a means of imprinting or directing the development of a unique and more functional community at maturity. These concepts, well-described by Yáñez-Ruiz et al. (2015), may hold some promise, but overcoming community inertia and resilience under any circumstance is not likely to be easy or straightforward (Figure 1).

Exploiting inter-animal variation in rumen microbial composition

Absent a clear pathway to overcoming rumen microbial community resilience to improve production, can we find a way to work variation in MCC among animals to our advantage? One strategy worth considering is using analysis of MCC as a tool to screen cows for predicted performance. Traits such as MPE are difficult to quantify, even under intensive testing (high-precision measurements over substantial time periods in tie stalls). If robust associations can be established between MPE (or the susceptibility to disorders, such as MFD or ruminal acidosis) and the abundance of specific taxa in easily collected samples (e.g., buccal swabs, Tapio et al., 2016), it would be possible to screen large numbers of animals and perhaps enable decisions of culling or group feeding that could improve overall productivity of a herd.

The relationship between resilience and functional redundancy

While rumen microbial community composition and its dynamics have received substantial attention of late, their importance must be kept in perspective. The community contains over a thousand OTU (a proxy for species), and their relative proportions vary greatly among cows. Yet, as pointed out by Taxis et al. (2015), the communities in different cows each work to convert a great variety of feeds to a remarkably similar suite of fermentation products that nourish the host. This is likely due to the fact that there exists a relatively small number of "degradation points" (substrates and hydrolysable linkages in biopolymers) and a commonality of catabolic pathways that can be distributed among this large number of species (Weimer, 2015). Few studies have examined resilience at both the microbial community and metabolic functional level, but it appears that the two largely run in parallel (Machado et al, 2015).

Conclusions

Evidence is accumulating that important dairy production metrics, such as milk production efficiency and milk composition, are associated with specific microbial taxa, and thus might be of interest as targets for community composition manipulation. However, healthy adult dairy cows display considerable individuality in the species composition of their rumen microbiota, and these communities display strong resilience upon perturbation. This will make difficult any directed manipulation of community composition, except in cases where open niches are available for colonization. Nevertheless, basic studies of the mechanisms underlying resilience may yield strategies for future modification of these communities (e.g., interventions conducted prior to weaning). Additionally, community composition analysis may inform decisions on herd management, such as group feeding or culling. To guide further advances, it is important that community composition not be viewed in isolation but must be tied to community function and an appreciation for functional redundancy of the community.

References

Allison, S.D, and J.B.H. Martiny. 2008. Resistance, resilience, and redundancy in microbial communities. Proc. Natl. Acad. Sci. USA 105:11512-11519. Doi: 10.1073/pnas.0801925105.

Chen, Y., J.J. Chen, and K.S. Creamer. 2008. Inhibition of anaerobic digestion process. Biores. Technol. 99:4044-4064. Doi.: 10:1016/jbiortech.2007.01.057.

Connor, E.E. 2015. Invited review: Improving feed efficiency in dairy production: Challenges and possibilities. Animal 9:395-408. Doi:10.1017/S1751731114002997.

Coyte, K.Z., J. Schluter, and K.R. Foster. 2015. The ecology of the microbiome: Networks, competition, and stability. Science 350:663-666. Doi:10.1126/science.aad2602.

deMenezes, A.B., E. Lewis, M. O'Donovan, B.F. O'Neill, N. Clipson, and E.M. Doyle. 2011. Microbiome analysis of dairy cows fed pasture or total mixed ration diets. FEMS Microbiol. Ecol. 78:256–265. Doi:10.1111/j.1574-6941.2011.01151.x

De Peters, E.J., and L.W. George. 2014. Rumen transfaunation. Immunol. Lett. 162: 69-76.

Gregg, K., B. Hamdorf, K. Henderson, J. Kopecny, and C. Wong. 1998. Genetically modified ruminal bacteria protect sheep from fluoroacetate poisoning. Appl. Environ. Microbiol. 64:3496-3498.

Grehan, M.J., T.J. Borody, S.M. Leis, J. Campbell, H. Mitchell, and A. Wettstein. 2010. Durable alteration of the colonic microbiota by the administration of donor fecal flora. J. Clin. Gastroenterol. 44:551-561.

Henderson, G., F. Cox, S. Ganesh, A. Jonker, W. Young, Global Rumen Census Collaborators, and P.H. Janssen. 2015. Rumen microbial community composition varies with diet and host, but a core microbiome is found across a wide geographical range. Sci. Reports 5:14567. Doi: 10.1038/srep14567

Herd, R.M., and P.F. Arthur. 2009. Physiological basis of residual feed intake. J. Anim.Sci. 87(E. Suppl.):E64-E71. doi:10.2527/jas.2008-1345
Jami, E., and I. Mizrahi. 2012. Similarity of the ruminal bacteria across individual lactating cows. Anaerobe 18:338-343.

Jami, E., B.A. White, and I. Mizrahi. 2014. Potential role of the bovine rumen microbiome in modulating milk composition and feed efficiency. PLoS One 9:e85423. Doi:10.1371/journal.pone.0085423.

Jewell, K.A., C. McCormick, C.L. Odt, P.J. Weimer, and G. Suen. 2015. Ruminal bacterial community composition in dairy cows is dynamic over the course of multiple lactations and correlates with feed efficiency. Appl. Environ. Microbiol. 81:4697-4710. Doi: 10.1128/AEM.00720-15.

Jones, R.J., and R.G. Megarrity. 1986. Successful transfer of DHP-degrading bacteria from Hawaiian goats to Australian ruminants to overcome the toxicity of *Leucaena*. Aust. Vet. J. 63:259-262.

Koch, R.M., L.A. Swiger, D. Chambers, and K.E. Gregory. 1963. Efficiency of feed use in beef cattle. J. Anim. Sci. 22:486-494.

Kofoid, C.S., and R.F. MacLennan. 1933. Ciliates from Bos Indicus Linn.III. Epidinium Crawley, *Epiplastron*, gen.nov., and Ophryoscolex Stein. Univ. Calif. Publ. Zool.39:1.

Lozupone, C.A., J.I. Stombaugh, J.I. Gordon, J.K. Jansson, and R. Knight. 2012. Diversity, stability and resilience of the human gut microbiota. Nature. 489:220-230. Doi: 10.1038/nature11550.

Lynch, S.V., and O. Pedersen. 2016. The human microbiome intestinal microbiome in health and disease. New Engl. J. Med. 375:2369-2379. Doi: 10.1056/NEJMra1600266

Machado, M.G., E. Detmann, H.C. Mantovani, S.C.Valadares Filho, C.B.P. Bento, M.I. Marcondes, and A.S. Assuncão. 2016. Evaluation of the length of adaptation period for changeover and crossover nutritional experiments with cattle fed tropical forage-based diets. Anim. Feed Sci. Technol. 222:132-148. Doi:10.1016/j.anifeedsci.2016.10.009

Mohammed, R., G.E. Brink, D.M. Stevenson, A.P. Neumann, K.A. Beauchemin, G. Suen, and P.J. Weimer. 2014. Bacterial communities in the rumen of Holstein heifers differ when fed orchardgrass as pasture versus as hay. Frontiers Microbiol 5:689. Doi: 10.3389/fmicb.2014.00689

Rico, D.E., S.H. Preston, J.M. Risser, and K.J. Harvatine. 2015. Rapid changes in key ruminal microbial populations during the induction of and recovery from diet-induced milk fat depression in dairy cows. Br. J. Nutr. 114: 358-367. Doi:10.1017/S0007114515001865

Rico, D.E, Y. Ying, A.R. Clarke, and K.J. Harvatine. 2014. The effect of rumen digesta inoculation on the time course of recovery from classical diet-induced milk fat depression in dairy cows. J. Dairy Sci. 97:3752-3760. Doi: 10.3168/jds.2013-7342

Shabat, S.K.B., G. Sasson, A. Doron-Faigenboim, T. Durman, S. Yaacoby, M.E. Berg Miller, B.A. White, N. Shterzer, and I. Mizrahi. 2016. Specific microbiome-dependent mechanisms underlie the energy harvest efficiency of ruminants. ISME J. Doi:10.1038/ismej.2016.62.

Tapio, I., K.J. Shingfield, N. McKain, A. Bonin, D. Fischer, A.R. Bayat, J. Vilkki, P. Taberlet, T.J. Snelling, and R.J. Wallace. 2016. Oral samples as non-invasive proxies for assessing the composition of the rumen microbial community. PLoS ONE 11(3): e0151220. Doi:10.1371/journal.pone.0151220

Taxis, T.M., S. Wolff, N.O. Minton, C. Zhang, J. Dai, R.D. Schnabel, J.F. Taylor, M.S. Kerley, J.C. Pires, W.R. Lamberson, and G.C. Conant. 2015. The players may change but the game remains: Network analyses of ruminal microbiomes suggest taxonomic differences mask functional similarity. Nucleic Acids Res. 2015:1. doi: 10.1093/nar/gkv973

Varel, V.H., J.T. Yen, and K.K. Kreikemeier. 1995. Addition of cellulolytic clostridia to the bovine rumen and pig intestinal tract. Appl. Environ. Microbiol. 61:1116-1119.

Weimer, P.J. 1998. Manipulating ruminal fermentation: A microbial ecological perspective. J. Anim. Sci. 76:3114-3122.

Weimer, P.J. 2015. Redundancy, resiliency and host specificity of the ruminal microbiome and their implications for engineering improved ruminal fermentations. Frontiers Microbiol. 6:296. doi: 10.3389/fmicb.2015.00296

Weimer, P.J., M.S. Cox, T. Vieira de Paula, M. Lin, M.B. Hall, and G. Suen. 2017. Transient changes in milk production efficiency and bacterial community composition resulting from near-total exchange of ruminal contents between high- and low-efficiency Holstein cows. J. Dairy Sci. 100:1765-1782. doi: 10.3168/jds.2017-12746

Weimer P. J., D. M. Stevenson, H.C. Mantovani, and S.L.C. Man. 2010a. Host specificity of the ruminal bacterial community of the dairy cow following near-total exchange of ruminal contents. J. Dairy Sci. 93:5902-5912.

Weimer, P.J., D.M. Stevenson, and D.R. Mertens. 2010b.Shifts in bacterial community composition in the rumen of lactating dairy cows under milk fat-depressing conditions. J. Dairy Sci. 93:265-278. doi:10.3168/jds.2009-2206.

Welkie, D.G., D.M. Stevenson, and P. J. Weimer. 2010. ARISA analysis of ruminal bacterial community dynamics in lactating dairy cows during the feeding cycle. Anaerobe 16:94-100.

Westman, W.E. 1978. Measuring the inertia and resilience of ecosystems. Bioscience 28:705-710.

Yáñez-Ruiz, D.R., L. Abecia, and C.J. Newbold. 2015. Manipulating rumen microbiome and fermentation through interventions during early life: A review. Front. Microbiol. 6:1133. Doi: 10.3389/fmicb.2015.01133.

Zhou, M., M. Hünenberg, K.A. Beauchemin, T.A, McAllister, E.K. Okine, and L.L. Guan. 2012. Individuality of ruminal methanogen/protozoa populations in beef cattle fed diets containing dried distillers' grains with solubles. Acta Agr. Scand. A - Animal Sci. 62:273-288. Doi: 10.1080/09064702.2013.788206

Table 1. Characteristics that describe the stability and adaptability of the ruminal microbial community.

Characteristic	Definition[1]	Likely status in the rumen
Inertia	Resistance to change	High, based on dosing studies
Resilience	Ability to restore its structure following acute or chronic disturbance	High, based on exchange studies
Components of resilience:		
Elasticity	Rapidity of restoration of a stable state following disturbance	Relatively high, based on exchange studies
Amplitude	Zone from which the system will return to a stable state	Very high, based on exchange studies
Hysteresis	Degree to which path of restoration is an exact reversal of path of degradation	Unknown
Malleability	Degree to which stable state established after disturbance differs from the original steady state	Low

[1] Verbatim definitions of Westman (1978).

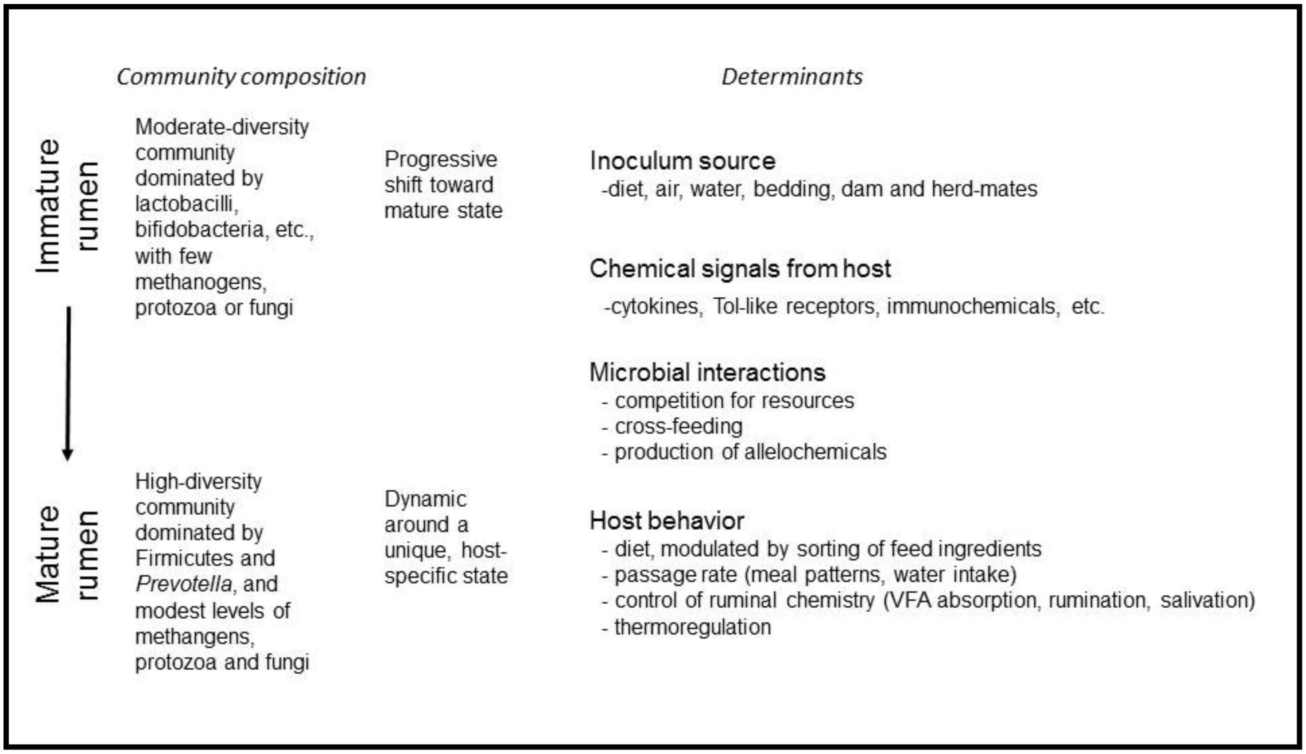
Table 2. Resilience of a rumen bacterial population following dietary change. Holstein heifers grazed orchardgrass pasture showed a shift in the abundance of Butyrivibrio, and the molar proportions of acetate and butyrate, when switched to orchardgrass hay; the effects were reversed when the heifers were returned to pasture. Heifers maintained on only pasture did not show these effects. Shifts in ruminal VFA profiles were consistent with observed shifts in Butryivibrio abundance. Values are means from last 3 days of 28-day periods. Data from Mohammed et al. (2014).

Heifer	Diet[1]	Relative abundance of Butyrivibrio in period[2]			Mol % Acetate in period			Mol % Butyrate in period		
		1	2	3	1	2	3	1	2	3
3274	PHP	15.3^{a}	6.9^{b}	10.8^{ab}	70.2^{b}	72.6^{a}	70.4^{b}	9.7^{a}	7.7^{b}	9.4^{a}
3292	PHP	13.5^{a}	6.1^{b}	10.2^{a}	63.8^{b}	71.7^{a}	67.7^{b}	11.1^{a}	7.9^{b}	10.5^{a}
3295	PHP	10.9^{a}	6.4^{b}	11.1^{a}	66.3^{b}	72.3^{a}	70.8^{ab}	11.6^{a}	7.7b	9.4^{ab}
3298	PPP	13.6	14.8	15.7	69.1	70.9	70.4	10.6	9.6	9.8
3412	PPP	19.6^{a}	18.6^{a}	13.7^{b}	69.5	71.0	70.1	10.1	9.2	9.1

[1] PHP=Heifers switched from pasture (period 1) to hay (period 2) then back to pasture (period 3). PPP=Heifers maintained on pasture throughout all 3 periods.

[2] Percent of 16S rRNA gene reads from next-generation sequencing (Roche 454). Data are averaged for liquid- and solids-associated communities, which were analyzed separately.

[a,b] Different letters between periods within heifer differ ($P < 0.05$).



Community composition

Determinants

Immature rumen

Moderate-diversity community dominated by lactobacilli, bifidobacteria, etc., with few methanogens, protozoa or fungi

Progressive shift toward mature state

Mature rumen

High-diversity community dominated by Firmicutes and *Prevotella*, and modest levels of methangens, protozoa and fungi

Dynamic around a unique, host-specific state

Inoculum source
-diet, air, water, bedding, dam and herd-mates

Chemical signals from host
-cytokines, Tol-like receptors, immunochemicals, etc.

Microbial interactions
- competition for resources
- cross-feeding
- production of allelochemicals

Host behavior
- diet, modulated by sorting of feed ingredients
- passage rate (meal patterns, water intake)
- control of ruminal chemistry (VFA absorption, rumination, salivation)
- thermoregulation

Figure 1. Comparison of the microbial community in the immature and mature rumen, along with factors that determine community composition. As the rumen matures, exogenous inoculation has less influence, and the adult community is shaped, and likely maintained, by a combination of microbial interactions and host behavioral adaptations.